

PROCEEDINGS  
OF THE  
CALIFORNIA ACADEMY OF SCIENCES

Vol. 48, No. 10, pp. 185-220, 6 figs., 5 tables

August 16, 1994

PHILIPPINE FROGS OF THE FAMILY RHACOPHORIDAE

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**ABSTRACT:** Philippine rhacophorid frogs include 18 species assigned to four genera. None of the genera but 12 of the species are endemic. Two species, *Philautus poecilus* and *P. surrufus*, are described as new. The distribution and ecology of the Philippine rhacophorids are discussed.

Received June 25, 1993. Accepted December 15, 1993.

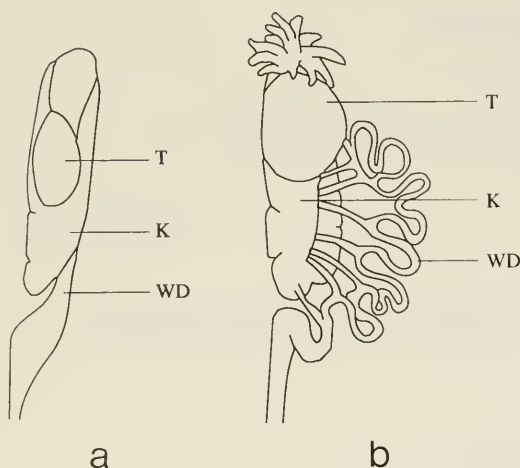
INTRODUCTION

The most recent systematic review of the Philippine rhacophorid frogs is that of Inger (1954). He referred the then known species to two genera, *Rhacophorus* (nine species) and *Philautus* (eight species). He did note, however, that the diagnoses of the genera were arbitrary and inadequate. Liem (1970) addressed that problem, providing a clearer understanding of the evolutionary trends within the Rhacophoridae and much more satisfactory diagnoses of the genera based on adult morphology. He assigned the Philippine species to four genera and redistributed some species between *Rhacophorus* and *Philautus*. Inger (1985b) reported that differences in the morphology and development of larvae further supported Liem's recognition of the genera *Hazelia* (= *Nyctixalus*) and *Philautus*, but that larval similarities only reaffirmed the close relationship of *Polypedates* and *Rhacophorus*.

Dring (1987) reexamined the Bornean *Philautus*, describing several new species and establishing species groups within the genus. Dubois (1987) recognized three subgenera of *Philautus* and two subgenera of *Rhacophorus*. As to *Philautus*, we have followed Dring's Group classification; and as to *Rhacophorus*, we have not placed the *R. bimaculatus* Group in a separate subgenus. Since 1954, extensive field surveys by the authors and others have greatly expanded the sample sizes for some of the Philippine species and have also provided samples from previously unknown populations on a number of islands. In view of these, a review of the Philippine rhacophorids is appropriate at this time.

MATERIALS AND METHODS

Type material, if available, has been examined. The largely unreported, extensive collections made by the authors over the past four



extent of webbing of fingers and toes, size-range of adults, digital disks, presence or absence of vomerine teeth and vocal sacs, nuptial pads, presence or absence of a cutaneous pectoris muscle, insertion of the lateralis externis muscle, type of eggs, and measurements such as snout-vent length (SVL), head length (HL), head breadth (HB), snout length (SnL), eye diameter (ED), tympanum diameter (TD), tibia length (TL), hindlimb length, third finger length (measured to proximal edge of basal tubercle), diameter of third finger disk, and diameter of third toe disk. These measurements were made to the nearest 0.1 mm, using a Helios dial-caliper. Ratios given in the descriptions are based on these measurements. Brief notes on color in life are given for species for which they are available. Only general habitat is noted in the species accounts. More information on habitats is provided in the section on ecology and zoogeography.

#### SYSTEMATIC SECTION

Rhacophoridae Hoffman  
 Polypedatidae Günther, 1859:9.  
 Rhacophoridae Hoffman, 1932 (1859):562

Under the provisions of Article 40 of the International Code of Zoological Nomenclature (Ride 1985), the name Rhacophoridae has priority over the name Polypedatidae Günther 1859, but it takes the date of Günther's publication. Whether the status of this taxon should be that of a subfamily of Ranidae, to which it is closely related, or a family equal in rank to Ranidae and Hyperolidae has been a matter of debate for the past century and a half. We follow Liem (1970), Dubois (1981), and Inger (1985) in recognizing the Rhacophoridae as a family.

#### KEY TO PHILIPPINE GENERA OF RHACOPHORIDAE

- 1a. Skin of dorsum and upper limb surfaces with prominent, pointed to spiny, scattered to numerous, whitish tubercles or pointed spicules; eggs pigmented, grayish to brownish ..... *Nyctixalus*
- 1b. Skin of dorsum and upper limb surfaces lacking prominent whitish tubercles or spicules; eggs whitish to creamy, without dark pigment ..... 2
- 2a. Vomerine teeth greatly reduced or absent; Wolffian ducts not convoluted (Fig. 1A);

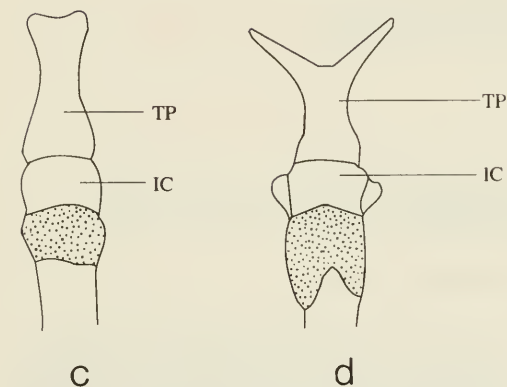


FIGURE 1. Male reproductive organ, ventral view (modified from Liem 1970); T = testis; K = kidney; WD = Wolffian duct: (a) *Philautus acutirostris*; (b) *Polypedates dugritei*. Distal phalanges of third finger, dorsal view (after Liem 1970); TP = terminal phalanx; IC = intercalary cartilage: (c) *Philautus acutirostris*; (d) *Polypedates colletti*.

decades and other recent collections, particularly those at the Field Museum and the United States National Museum, have also been studied.

Repositories for specimens are referred to in the text by the following standard acronyms: ANSP, BMNH, CAS, CAS-SU, CM, FMHN, MNHN, MCZ, MSNG, MTKD, NMW, SMF, USNM, ZMB (Leviton *et al.* 1985). Except for the new species, specimens examined are cited in Appendix B rather than in species accounts.

Characters used to differentiate species include: color features, cutaneous ornamentation,

- terminal phalanx of digits notched or bluntly rounded (Fig. 1C) ..... *Philautus*
- 2b. Vomerine teeth prominent; Wolffian ducts convoluted (Fig. 1B); terminal phalanx of digits Y-shaped (Fig. 1D) ..... 3
- 3a. Skin on head partly co-ossified with skull; head longer than broad; dorsal color pattern usually dull grayish with various dark markings; vertebral column diplasiocoelous (sacral vertebra convex anteriorly with double condyle posteriorly; eighth vertebra biconcave, and first seven procoelous) ..... *Polypedates*
- 3b. Skin of head free from skull; head as broad as or broader than long; dorsal color pattern bright green or brownish; vertebral column procoelous (vertebrae concave at anterior face and convex at posterior face) ..... *Rhacophorus*

**Nyctixalus Boulenger**

*Nyctixalus* Boulenger, 1882b:35. Type species: *Nyctixalus margartifer*, by monotypy.  
*Hazelia* Taylor, 1920:292 (not *Hazelia* Walcott, 1920:281).  
 Type species: *Hazelia spinosa*, by original designation.  
*Edwardtayloria* Marx, 1975:2. Nomen substitutum for *Hazelia* Taylor, 1920.

Dubois (1981) resurrected the genus *Nyctixalus* from the synonymy of *Philautus* and referred four, possibly five, species to it, four that Liem (1970) had placed in the genus *Hazelia* and one from the genus *Theloderma* as possibly belonging in *Nyctixalus*. Inger (1985a) recognized only three species as belonging in *Nyctixalus* (*margartifer*, *pictus*, and *spinusus*).

DIAGNOSIS.—Size moderate (SVL 30–40 mm at maturity for Philippine species); skin of dorsal surfaces with blunt or sharply pointed spicules; belly coarsely granular; disks of fingers large, completely circumscribed by groove; fingers without or only with basal webs; tips of digits with prominent disks, those of toes smaller than those of fingers; hindlimbs much longer than body; toes one-third to one-half webbed; outer metatarsals not fused; males have nuptial pads; Wolffian ducts not convoluted; no vomerine teeth; males without vocal sacs; terminal phalanges Y-shaped; omosternum forked; humero-dorsalis muscle two slips; eggs large, heavily pigmented; clutch size 10–30 (for Philippine species), eggs deposited on walls of tree holes; feeding-larval stages are flatter in lateral view than larvae of other rhacophorid genera (Inger 1985b).

KEY TO PHILIPPINE SPECIES  
 OF *NYCTIXALUS*

- 1a. Cranial and supratympanic crests present; numerous, pointed, whitish spicules covering dorsal surfaces; posterior surface of thighs with coarse granules ..... *N. spinusus*
- 1b. Cranial and supratympanic crests absent; scattered, low, whitish tubercles covering dorsal surfaces; posterior surface of thighs nearly smooth ..... *N. pictus*

***Nyctixalus pictus pictus* (Peters)**

*Ixalus pictus* Peters, 1871:580 (type loc.: Sarawak, Borneo; holotype in MSNG).  
*Philautus anodon*: van Kampen 1923:271.

DESCRIPTION.—SVL 30.4–34.5 for two males; HB 96–99% of HL and 34–37% of SVL; snout nearly truncate, jutting sharply at level of nostrils, SnL 41% of HL and 42% of HB; eye moderate, ED 67–74% of SnL and 25–32% of HB; tympanum fully exposed, TD 66–85% of ED; canthus sharply rounded; lores nearly vertical, shallowly concave; fingers without webs; diameter of third finger disk 25–27% of third finger length and 54–61% of TD; subarticular tubercles low, slightly rounded; supernumerary tubercles present; inner metacarpal tubercle poorly defined; SVL 61–62% of hindlimb length; TL 56–58% of SVL; toes webbed: to distal edge of tubercle on first, between tubercle and disk on inside of second, to tubercle on third, and nearly to basal tubercle on fourth; diameter of third toe disk 71% of third finger disk; subarticular tubercles low, slightly pointed; metatarsal tubercles present; prominent inner but no outer metatarsal tubercle; skin of dorsum and limbs with scattered low, whitish tubercles; underside of head and throat nearly smooth; belly with flat granules; prominent tubercle on both sides dorsolateral to vent, and several below vent.

COLOR.—In preservative, tan on upper surfaces with scattered, brown-ringed, whitish spots concentrated along upper lip, upper eyelid, canthus, and tip of snout, a large one dorso-posterior to tympanum; venter creamy white. In life, the dorsal color is cinnamon-brown to chocolate (Inger 1966).

COMPARISONS.—The Palawan population, based on two examples, is judged conspecific with samples of *Nyctixalus p. pictus* from northern Borneo. This species differs from *N. spinusus* from the southeastern Philippines in the less numer-

ous and less prominent dorsal tubercles, the lack of prominent cranial and supratympanic crests, less numerous whitish spots, and slightly broader head relative to SnL or HL.

**REPRODUCTION.**—This species attaches its eggs to walls of tree holes about 5–10 cm above the water level in lowland forest in north Borneo (Inger 1966). Larvae at pre-limb bud (pre-stage 25, Gosner 1960) stages also occur in similar tree-hole sites (Inger 1985b). One of the specimens, laboratory-reared to early metamorphosis, confirms the identification of the larvae. Gravid females from the Bornean population exhibit a low number (8–10) of large grayish eggs. Neither egg-deposition site nor larvae have been observed for the Philippine population.

**HABITAT.**—The two known Philippine specimens are from lowland forest at 150–300 m elevation.

**RANGE.**—Malay, Singapore, Borneo, and Palawan Island, Philippines.

### *Nyctixalus spinosus* (Taylor)

*Hazelia spinosa* Taylor, 1920:292 (type loc.: Bunawan, Agusan Prov., Mindanao Island; holotype in CM); 1921:93; Liem 1970:95.

**DESCRIPTION.**—SVL 30.4–37.2 mm for seven males and 36.8–39.0 mm for four females; HB 88–94% of HL and 34–39% of SVL; snout nearly truncate to obtusely pointed, jutting out at level of nostrils; SnL 39–44% of HL and 43–50% of HB; ED 68–86% of SnL and 31–38% of HB; tympanum bordered by supratympanic crest; TD 60–80% of ED; canthus sharply rounded; lores nearly vertical, slightly concave; fingers without webs; diameter of third finger disk 23–29% of third finger length and 53–70% of TD; subarticular tubercles round-pointed; supernumerary tubercles prominent; large inner metacarpal tubercle, SVL 56–61% of hindlimb length; TL 56–61% of SVL; toes webbed: to tubercle on first toe, beyond tubercle on inside of second, between basal and distal tubercle on third, nearly to proximal tubercle on fourth, and to base of tubercle on fifth; diameter of third toe disk 57–75% of third finger disk; subarticular tubercles round-pointed; supernumerary tubercles numerous; prominent inner but no outer metatarsal tubercle; skin of dorsum and limbs with prominent, pointed, whitish spicules; cranial and supratympanic crests present; underside of head and throat with small granules; belly and pos-

terior thighs coarsely granular; whitish tubercle dorso-lateral to vent on both sides and several tubercles below vent.

**COLOR.**—In preservative, pinkish gray to tan or light brown on upper surfaces with a pair of prominent, whitish, brown-rimmed spots dorso-posterior to the tympanum and usually a few scattered, similar but smaller spots on dorsum, hindlimbs, canthus, snout, and sometimes the edge of upper eyelid; venter creamy white.

In life, dorsum reddish to tannish brown with a pair of prominent white spots dorsolaterally at shoulder level and a few smaller, scattered white spots posteriorly; several short, white, transverse bars on hind limbs.

**REPRODUCTION.**—Three adults and about 120 tadpoles in a water-containing hole near the base of the trunk of an *Agathis alba* tree located in the dipterocarp forest on Dapitan Peak, Mindanao Island, are identified with this species (Alcala and Brown 1982). The three adults clung to the charred wood above the level of the water. The larval stages varied from 1–44 (Gosner 1960), indicating that multiple clutches were laid at different times. Color markings, dorsal spicules and webbing of toes, evident in late stages, positively identify the larvae with this species. Because gravid females have 30–40 eggs per clutch, the number of egg-depositions was probably four or five. The mature eggs from gravid females are brownish on one hemisphere and black on the other.

Although not observed, the egg-deposition site is probably on walls of tree holes above the water level as has been reported for the closely related *Nyctixalus pictus* (Inger 1966).

**COMPARISONS.**—See *Nyctixalus pictus*.

**HABITAT.**—Specimens are from dipterocarp forest areas at elevations of 500–1100 m.

**RANGE.**—Basilan, Mindanao, and Bohol islands.

### *Philautus* Gistel

*Orchestes* Tschudi, 1838:35 (not Illiger, 1798:498). Type species: *Hyla aurifasciata* Schlegel, 1837, by monotypy.

*Ixalus* Duméril and Bibron, 1841:523 (not Ogilby, 1837:119). Nomen substitutum for *Orchestes* Tschudi, 1838.

*Philautus* Gistel, 1848:10. Nomen substitutum for *Orchestes* Tschudi, 1838.

Liem (1970) redefined the genus *Philautus* and assigned to it three species that had been previously placed in *Rhacophorus* (*emembranatus*, *lissobrachiis*, and *surdus*). Dring (1987) further

TABLE 1. Snout-vent length and pertinent body proportions for Philippine species of the *aurifasciatus* group of *Philautus*. (R = range, M = mean, n = number in sample, 3fd = third finger disk, 3fl = third finger length, 3td = third toe disk.)

Species	Adult SVL		ED HB	TD ED	3fd 3fl	3td 3fd
	Male	Female				
<i>P. acutirostris</i>						
R	16.1–22.7	22.0–27.8	0.31–0.38	0.35–0.50	0.36–0.46	0.80–0.97
M			0.342	0.422	0.423	0.897
n	15	17	16	16	16	12
<i>P. leitensis</i>						
R	19.2–21.9	22.6–26.4	0.23–0.35	0.29–0.50	0.26–0.44	0.68–0.92
M			0.283	0.381	0.312	0.787
n	10	12	12	12	12	12
<i>P. longicus</i>						
R	18.0–21.9	21.2–25.5	0.27–0.33	0.15–0.29	0.19–0.29	0.40–0.71
M			0.301	0.214	0.246	0.587
n	12	24	15	15	15	15
<i>P. schmackeri</i>						
R	19.0–21.5	22.6–28.0	0.25–0.34	0.16–0.35	0.15–0.28	0.50–0.71
M			0.291	0.21	0.225	0.624
n	14	15	18	18	18	18

divided the Bornean and Philippine *Philautus* into species-groups (*hosei*, *vermiculatus*, *surdus*, *tectus*, and *aurifasciatus*). Further discussion of these species groups was provided by Inger (1989). Both Dring and Inger referred the then known Philippine species to the *surdus* and *aurifasciatus* groups.

DIAGNOSIS.—Size small to moderate (SVL 16–44 mm at maturity for known Philippine species); body tapered from widest point of head to groin, skin of dorsum shagreened with or without tubercles, belly with flattish granules; digital disks moderate to large, completely circumscribed by a groove, disks of toes somewhat smaller than those of fingers; fingers without or only with basal webs; nuptial pads present or absent; hindlimb much longer than body; toes moderately to almost fully webbed; vomerine teeth present or absent; usually males with vocal sacs; terminal phlanges notched or bluntly rounded; omosternum usually not forked at base; Wolffian ducts not convoluted; petrohyoideus posterior muscle usually two slips; eggs large, unpigmented; clutch size 6–30 (Philippine species); eggs, where known, deposited in leaf axils, epiphytic ferns, and *Nepenthes* pitchers; development direct, within egg capsule for all species for which development is known.

This montane genus, with nine species, exhibits greater diversity than other rhacophorid genera occurring in the Philippines.

KEY TO THE PHILIPPINE SPECIES OF  
*PHILAUTUS*

- 1a. SVL for mature males usually less than 23 mm, for females less than 28 mm; vomerine teeth usually absent ..... 2
- 1b. SVL for mature males usually greater than 23 mm, for females greater than 28 mm; vomerine teeth usually present ..... 5
- 2a. Diameter of third toe disk rarely less than 70% of third finger disk; TD usually greater than 35% of ED, (Table 1); except occasionally for *P. leitensis*, upper eyelids and dorsum without tubercles (or very rarely a few); dorsal color pattern not exhibiting a dark cruciform blotch ..... 3
- 2b. Diameter of third toe disk rarely greater than 70% of third finger disk; TD very rarely as great as 35% of ED (Table 1); dorsum with some tubercles at least on eyelids and a pair at shoulder level; dorsal color pattern usually with some modification of dark cruciform blotch ..... 4
- 3a. SnL usually greater than 40% of HB; snout sharply pointed, often with pale-colored projection at tip; webbing of fourth toe usually does not reach tubercle (Fig. 3A); (known from Mindanao and Basilan islands) ..... *P. acutirostris*
- 3b. SnL usually less than 40% of HB; snout round pointed, without pale-colored pro-

TABLE 2. Snout-vent length and pertinent body proportions for species of the *surdus* group of *Philautus* and *P. poecilus*. (R = range, M = mean, n = number in sample, 3fd = third finger disk, 3fl = third finger length, 3td = third toe disk.)

Species	Adult SVL		ED HB	TD ED	3fd 3fl	3td 3fd
	Male	Female				
<i>P. emembranatus</i>						
R	25.1–32.4	30.9–43.9	0.25–0.31	0.18–0.34	0.22–0.36	0.65–0.86
M			0.29	0.255	0.281	0.771
n	7	8	15	15	15	15
<i>P. surdus</i>						
R	22.5–31.0	28.5–38.4	0.30–0.37	0.32–0.49	0.36–0.45	0.83–1.00
M			0.34	0.379	0.403	0.912
n	25	20	25	25	25	25
<i>P. surrufus</i>						
R	20.0–27.6	26.6–35.4	0.31–0.39	0.34–0.50	0.34–0.44	0.81–1.00
M			0.35	0.437	0.379	0.909
n	16	12	20	20	20	20
<i>P. poecilus</i>						
R	21.4–28.1		0.28–0.32	0.23–0.38	0.21–0.38	0.64–0.80
M			0.296	0.267	0.333	0.723
n	7		7	7	7	7

jection at tip; webbing of fourth toe usually to proximal edge of tubercle (Fig. 3B); (known from Leyte and Bohol islands) ...

- ..... *P. leitensis*
  - 4a. Dorsum heavily shagreened, with prominent tubercles at shoulder level on both sides and on eyelids, usually other scattered tubercles; (known from Mindoro Island) ..... *P. schmackeri*
  - 4b. Dorsum usually with tubercles in blackish blotch at shoulder level on both sides and on eyelid, rarely with other scattered tubercles; (known from Palawan and Borneo) ..... *P. longicrus*
  - 5a. Dorsum with pair of distinct tubercles in darkly pigmented spots at shoulder level; other scattered tubercles on eyelids and dorsum; diameter of third finger disk usually greater than 35% of third finger length; all toes but fourth usually webbed to between tubercle and disk (Fig. 4B); (known from Greater Mindanao and Greater Luzon areas) ..... *P. surdus*
  - 5b. Dorsum relatively smooth, usually without or with very few tubercles; webs of toes usually not distal to tubercles except on second and fifth for some specimens of *emembranatus* ..... 6
  - 6a. Dorsal color pattern usually mottled black (or dark brown) and ivory or tannish (Fig. 2A), or with dark cruciform blotch; SVL for adult males 21–28 mm (Table 2); diameter of third finger disk usually less than 35% of third finger length; (known from northeastern Mindanao Island) ..... *P. poecilus*
  - 6b. Dorsal color pattern reddish brown or mottled reddish brown and tannish (Fig. 2B); ED greater than 30% of HB; diameter of third finger disk usually greater than 35% of third finger length; SVL for adult males 20–28 mm (Table 2); (known from northwestern Mindanao Island) ..... *P. surrufus*
  - 6c. Dorsal color pattern golden-brown to gray, usually not heavily blotched; ED usually less than 30% of HB; diameter of third finger disk usually less than 35% of third finger length; SVL for adult males 25–33 mm (Table 2); (known from Mindanao Island) ..... *P. emembranatus*
- Inger (1954) regarded four Philippine species (*acutirostris*, *leitensis*, *longicrus*, and *schmackeri*) as probably closely related. Later (1966) he placed *acutirostris*, *longicrus*, and the Bornean species *petersi* and *mjobergi* in the synonymy of *aurifasciatus*, but he did not comment on the status of *leitensis* or *schmackeri*. Dring (1987) resurrected all of these species and restricted *aurifasciatus* to Java. He also extended the range of *longicrus* to include some populations in north-

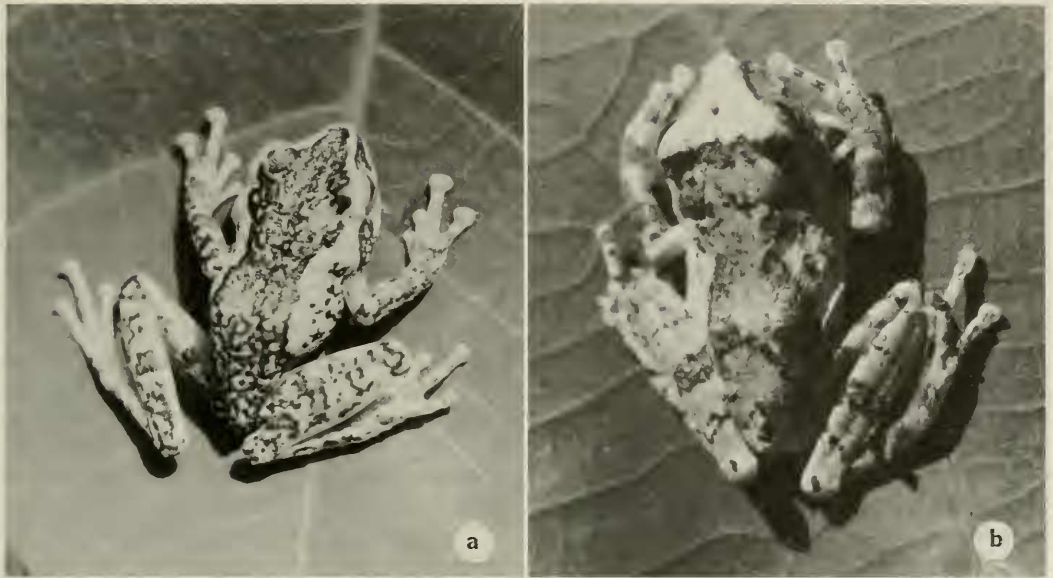


FIGURE 2. (a) *Philautus pocillus* (23 mm SVL); (b) *Philautus surrufus* (28 mm SVL).

west Borneo as well as Palawan. He further noted the general similarities between *longicrus* and *mjobergi*.

#### AURIFASCIATUS GROUP

Dring (1987) defined the *aurifasciatus* Group as: small to moderate in size, vomerine teeth absent, cutaneous pectoris muscle present, geniohyoideus lateralis externis insertion includes membrana thyroideus, nuptial pad small and smooth, and ova unpigmented. He assigned four Philippine species (*acutirostris*, *leitensis*, *longicrus*, and *schmackeri*) to this group.

Liem (1970) stated that these species lack a nuptial pad, because he did not find it for specimens that he examined. We found small to moderate pads for males of *P. acutirostris* and *P. longicrus*, but large for *P. schmackeri*. The nuptial pad is evident for only some of the males of any of these species. This may be seasonal or caused by some other regulating mechanism. We found vomerine teeth present for most examples of *P. acutirostris* but lacking for other Philippine species of this group.

#### *Philautus acutirostris* (Peters)

*Ixalus acutirostris* Peters, 1867:32 (type loc.: Eastern Mindanao, Philippines; holotype in ZMB).

*Philautus woodi* Stejneger, 1905:346 (type loc.: Mt. Apo, Mindanao I., Philippines; holotype in USNM).

*Rhacophorus (Philautus) woodi*: Ahl 1931:66.

*Philautus basilanensis* Taylor, 1922a:169 (type loc.: Basilan Island; holotype in CAS).

We examined the holotypes of *Ixalus acutirostris*, *Philautus basilanensis*, and *Philautus woodi* and found them to be, for characters used, within the range of variation exhibited by a large sample of the *P. acutirostris* populations in northeastern and northwestern Mindanao. Our findings are in agreement with those of Inger (1954), and we treat both names as synonyms of *acutirostris*.

**DESCRIPTION.**—Body tapering posteriorly; SVL 16.1–22.7 mm for 15 males and 22.0–27.8 for 17 females (The holotype at 17 mm SVL and lacking vocal slits is assumed to be an immature female.); HB 99–108% of HL and 39–44% of SVL; obtusely to acutely pointed, frequently with narrowly rounded, pale-colored projection at tip of snout; SnL 41–47% of HL and 39–46% of HB; eye moderate, ED 76–97% of SnL and 31–38% of HB; tympanum distinct, bordered dorsally by shallow fold extending from corner of eye to axilla, TD 35–50% of ED; canthus moderately to sharply rounded; lores somewhat oblique, concave; vomerine teeth present; males with vocal sacs; fingers without webs; diameter of third finger disk 39–46% of third finger length and 118–156% of TD; subarticular tubercles low, rounded, nearly as broad as fingers except for basal one

on third toe; palmer area coarsely granular; an elongate inner metacarpal tubercle and usually a less distinct outer one; nuptial pad of males, small rounded, smooth; SVL 49–67% of length of hind-limb; tibia length 59–69% of SVL; toes webbed: at most to distal edge of subarticular tubercle on first and second, to middle or outer edge of distal subarticular tubercle on outside of third and inside of fifth, and to penultimate tubercle on fourth (Fig. 3A); diameter of third toe disk 80–97% of diameter of third finger disk; plantar nearly smooth or with some low tubercles; elongate inner but no outer metatarsal tubercle; outer edge of fifth toe smooth or with fringe of low tubercles; skin of dorsum shagreened, usually without tubercles, or with a few low tubercles, most prominent for males; belly, undersurface of thighs, and to lesser extent posterior thighs coarsely granular; under surface of head and throat finely granular to nearly smooth.

**COLOR.**—In preservative, dorsal ground color variable, from grayish tan to reddish brown, or sometimes sooty gray-brown; nearly uniform, or with a darker interorbital area and sometimes small, dark blotches associated with tubercles; lores and tympanic area usually somewhat darker than dorsum; posterior surface of thighs and lower leg, anterior surface of thighs and groin rusty-brown; upper surface of hindlimbs with or without vague dark, transverse barring; sometimes tip of snout, canthus, border of upper eyelid, and/or supratympanic fold pale relative to rest of dorsum; venter creamy to ivory with some brownish blotches, usually most prominent under head and throat.

In life, usually dorsum and limbs grayish brown, lilac-brown, or reddish brown nearly uniform (rarely with darker hourglass pattern); darker on lateral surface of head.

**REPRODUCTION.**—Gravid females of *P. acutirostris* possess 5–10 large non-pigmented eggs in each ovary, thus a clutch size of 10–20 eggs. Several clutches of very similar eggs were in leaf axils of wild banana and aerial ferns on Dapitan Peak in western Mindanao in 1959 and on Mt. Hilonghilong in eastern Mindanao in 1971 (Alcala and Brown 1982) and may belong to this species. Lack of late developmental stages precluded positive identification although the series of early stages were similar to those of other members of the genus *Philautus*.

**COMPARISONS.**—*Philautus acutirostris* is very similar to and doubtless related to *P. leitensis*.

The color patterns are similar, and SVL for both sexes exhibit essentially the same range. *Philautus acutirostris* differs in: the less extensive webbing of the toes (Figs. 3A, B); the more pointed, longer snout relative to HB, usually exhibiting a pale-colored projection at the tip; and the somewhat smaller eye relative to the HB (Table 1). *Philautus acutirostris* differs from *longicrus* in: the lack of tubercles on the dorsum, the larger tympanum relative to the eye, and the more expanded finger disks relative to finger length.

**HABITAT.**—Based on 90 specimens from Dapitan Peak on Zamboanga Peninsula and Mt. Hilonghilong in northeastern Mindanao, *P. acutirostris* ranges from about 400 m in dipterocarp forest to more than 2000 m in montane forest.

**RANGE.**—Basilan and Mindanao islands, Philippines.

### *Philautus leitensis* (Boulenger)

*Ixalus leitensis* Boulenger, 1897:107 (type loc.: Leyte Island, Philippines; holotype in BMNH).

Boulenger (1897) described this species from Leyte Island, based on a single specimen. Stejneger (1905), Taylor (1920) and Inger (1954) continued to recognize the species but with few or no additional specimens on which to determine variability or assess relationships to other species. Our series from Bohol and one specimen from Leyte are in general agreement with the holotype and serve to establish the differences that we use to distinguish it from *P. acutirostris*. These species are closely related and may simply represent geographic races (subspecies). However, pending the availability of more material from Leyte (type locality) as well as Samar and possibly small islands between them and Mindanao, we continue to treat *leitensis* as a distinct species.

**DESCRIPTION.**—SVL 19.2–21.9 mm for 10 males and 22.6–26.4 mm for 12 females; HB 103–111% of HL and 38–43% of SVL; snout rounded to round pointed, SnL 36–45% of HL and 34–41% of HB; eye large, ED 68–93% of SnL and 23–35% of HB; tympanum distinct, bordered dorsally by shallow fold, TD 29–50% of ED; canthus sharply rounded; lores slightly oblique, usually somewhat concave; vomerine teeth absent; fingers without webs; diameter of third finger disk 26–44% of third finger length and 96–140% of TD (only two of 15 specimens below 109%); subarticular tubercles prominent, outer tubercle



low, oval to elongate; nuptial pad small, round, smooth; SVL 49–62% of hindlimb length; TL 55–66% of SVL; toes webbed: to between subarticular tubercle and disk on inside of first, second, third and fifth, and to distal edge of penultimate tubercle on fourth toe (Fig. 3B); diameter of third toe disk 68–92% of third finger disk; subarticular tubercles moderate, low; few small, supernumerary tubercles; inner metatarsal tubercle present; no outer tubercle; skin of dorsum shagreened, very rarely with few tubercles; undersurface of head and throat relatively smooth, except for low, whitish tubercles along border of lower jaws for most specimens; belly and posterior surface of thigh with flattish granules.

**COLOR.**—In preservative, dorsum and upper lateral surfaces grayish-tan or tan to dark brown, nearly uniform, sometimes with a few small dark spots or rarely lighter blotches; venter pale ivory to creamy usually with brownish flecks or heavily mottled with brown especially under head and throat; posterior and anterior surface of thighs rusty-brown, extending onto the lateral surface at the groin.

In life, dorsal ground color orange-brown, reddish brown, or lilac-brown, nearly uniform or with some darker spots; hindlimbs usually with dark crossbars.

**REPRODUCTION.**—Three gravid females with greatly enlarged, non-pigmented eggs in the ovaries provide a clutch size of 6–14.

**COMPARISONS.**—See *Philautus acutirostris*. *Philautus leitensis* also differs from *longicrus* and *schmackeri* in the larger tympanum relative to the eye (Table 1) and the less tuberculate dorsum.

**HABITAT.**—All Bohol specimens came from dipterocarp or submontane forest at elevations between 150 and 700 m.

**RANGE.**—Leyte and Bohol islands, Philippines.

### *Philautus longicrus* (Boulenger)

*Exalus longicrus* Boulenger, 1894:88 (type loc.: Palawan Island; syntypes in BMNH).

**DESCRIPTION.**—SVL 18.0–21.9 mm for 12 males and 21.2–25.5 for 24 females (one female, 19.9 mm, is probably mature, based on appearance of oviduct); HB 106–117% of HL and 39–44% of SVL; snout rounded to round-pointed, protruding but without pale, conical tip, SnL 30–36% of HB and 33–41% of HL; eye large; ED

83–100% of SnL and 27–33% of HB; tympanum covered by skin, TD 15–29% of ED; canthus sharply to moderately rounded; lores slightly oblique and concave; vomerine teeth absent; males with vocal sacs; fingers without webs; diameter of third finger disk 19–29% of third finger length and 140–233% of TD; subarticular tubercles round to round-pointed; a few, low supernumerary tubercles; elongate inner metacarpal tubercle; low fringe on outside of fourth finger; lower arm smooth; nuptial pad small, nearly round, smooth; SVL 52–59% of hindlimb length; TL 57–64% of SVL; toes webbed: at most nearly to disk on inside of first and second, to tubercle or its midpoint on inside of third and fifth, short of penultimate tubercle on fourth (Fig. 3C); diameter of third toe disk 40–71% of diameter of third finger disk; subarticular tubercles rounded, small, low; supernumerary tubercles few and small or absent; inner metatarsal tubercle elongate, outer small or absent; skin of dorsum shagreened, nearly uniform or with a few scattered, small tubercles; under surface of head and throat nearly smooth to faintly granular (especially for males); usually some tubercles on edge of lower jaw; belly and proximal under surface of thighs coarsely granular.

**COLOR.**—In preservative, dorsal ground color grayish or grayish tan to brown or dark brown, nearly uniform or with scattered dark or pale spots (24 of 60), with pale, median band (4 of 60), or with dark cruciform or hourglass pattern (32 of 60); hindlimbs usually with dark crossbars; posterior and anterior surface of thighs with reddish-brown bands and sometimes similarly colored blotches on posterior lateral surfaces; venter cream to creamy tan usually with small, dark flecks under head and throat and sometimes brown spots or blotches on belly.

In life, dorsum nearly uniformly dark brown (sometimes almost black) or ochre-brown with a darker hourglass spot or blotches; snout area usually more pale; hind limbs usually with blackish transverse bars; lateral surfaces lighter brown; hindlimbs with dark cross bars.

**REPRODUCTION.**—Two gravid females have 9 and 13 large, non-pigmented eggs in the ovaries.

**COMPARISONS.**—*Philautus longicrus* differs from *schmackeri* in: more extensive webbing of toes (Fig. 3C, D); slightly less prominent tubercles on dorsum; and the slightly larger eye relative to SnL. See **COMPARISONS** under *P. acutirostris* and *P. leitensis*.

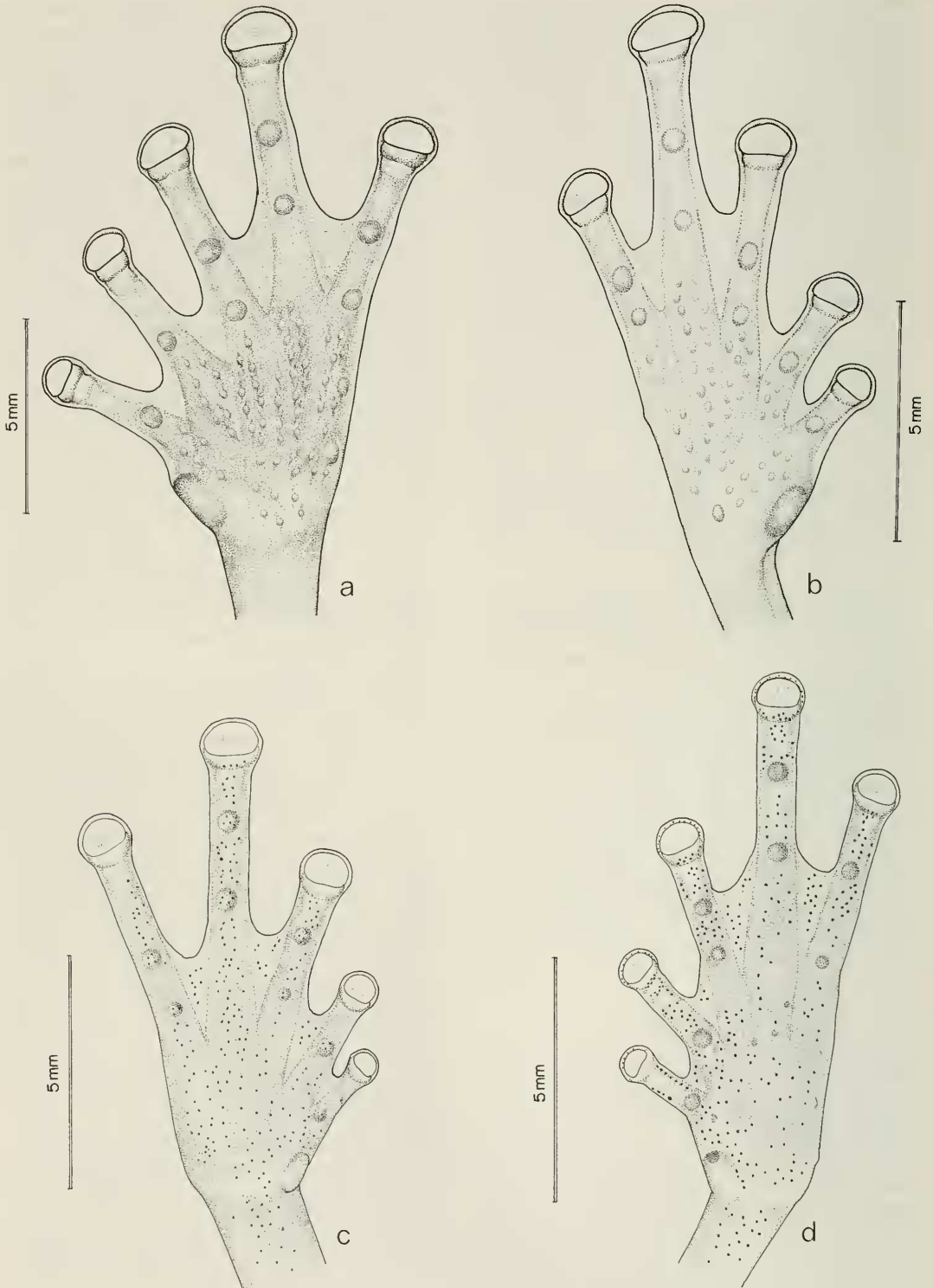


FIGURE 3. Ventral surface of foot, showing extent of webbing and tubercles: (a) *Philautus acutirostris*; (b) *Philautus leitensis*; (c) *Philautus longicrus*; (d) *Philautus schmackeri*.

**HABITAT.**—This species occurs from near sea level in dipterocarp forest to nearly 1300 m in montane forest on Thumb Peak. *Philautus longicrus* occurs in moss forest at 3,000 m in north-west Borneo (Inger and Stuebing 1992).

**RANGE.**—Borneo and Palawan Island, Philippines.

### *Philautus schmackeri* Boettger

*Philautus schmackeri* Boettger, 1892:17 (type Loc.: Mount Halcon, Mindoro Island; holotype in SMF).

*Ixalus mindorensis* Boulenger, 1897:107 (type loc.: Mount Dulangan, Mindoro Island; syntypes in BMNH).

**DESCRIPTION.**—SVL 19.0–21.5 mm for 14 males and 22.6–28.0 mm for 15 females; HB 100–111% of HL and 38–44% of SVL; snout round pointed without conical tip, SnL 38–44% of HL and 31–41% of HB; eye moderate, ED 68–93% of SnL and 25–34% of HB; tympanum covered by skin, TD 16–35% of ED; canthus sharply rounded; lores slightly oblique and concave; vomerine teeth absent; males with vocal sacs; fingers without distinct webs; diameter of third finger disk 15–28% of third finger length and 100–225% of TD; subarticular tubercles rounded; supernumerary tubercles few and small; elongate inner and outer metacarpal tubercles; low flange of skin on outer edge of hand; row of pale tubercles along lower arm; nuptial pad small, round, smooth; SVL 54–63% of hindlimb length; TL 53–60% SVL; toes webbed: at most to distal edge of tubercle or beyond on inside of first, second, and third, usually to middle or distal edge of tubercle on third and fifth, and to penultimate tubercle on fourth (Fig. 3D); diameter of third toe disk 50–71% of third finger disk; subarticular tubercles rounded, small, low; scattered small tubercles on plantar surface; an outer but no inner metatarsal tubercle; skin of dorsum shagreened, uniform or with few scattered tubercles; undersurface of head and throat nearly smooth or with fine granules; belly and posterior thighs with longer, flattish granules.

**COLOR.**—In preservative, highly variable; dorsal ground color grayish-tan, tan, brown, dark brown and reddish brown; relatively uniform or with scattered dark or pale spots (19 of 60), with pale, median dorsal band (15 of 60), or with dark cruciform or hourglass pattern (26 of 60); limbs with vague to distinct, dark transverse bands or rarely nearly uniformly dark; a rusty-red, longitudinal band on posterior and anterior surface of thighs; venter pale cream to creamy tan, usu-

ally with dark flecks (especially anteriorly), or with scattered, more dense brownish spots.

In life, dorsal ground color light brown to dark brown with variable, scattered, dark or pale markings; lateral surfaces to dorsolateral line tannish anteriorly, usually darker posteriorly; dark transverse bars on hindlimbs and interorbital region.

**REPRODUCTION.**—Clutch size varies from 6–15 for this species, based on the number of enlarged ovarian eggs in several gravid females and two clutches of 12 and 15 embryos, respectively, from leaf axils of bird's nest ferns (Alcala and Brown 1982). The oldest larva in these clutches was about stage 31 (Gosner 1960). The examples are typical of that stage in other species of the genus *Philautus*.

**COMPARISONS.**—See *Philautus longicrus* and *acutirostris*. In terms of the tuberculation of the dorsum and the extent of the webbing of the toes, *Philautus schmackeri* is more similar to *P. surdus* than it is to *P. longicrus*, *aurifasciatus*, or *acutirostris*. *Philautus schmackeri*, however, was reported by Liem (1970) as being more closely related to *P. aurifasciatus* (and presumably *longicrus*), being in agreement for all 36 character states; whereas *P. schmackeri* differs from *surdus* (= *lissobranchius* of Liem) in the character state for the geniohyoideus muscle, the vomerine teeth (not absolute), and the smaller size. We have followed Liem in including *schmackeri* in the *aurifasciatus* group.

**HABITAT.**—Specimens of *Philautus schmackeri* occur from lower dipterocarp to montane forests at elevations from 30–1450 m.

**RANGE.**—Mindoro Island, Philippines.

### VERMICULATUS GROUP

Dring (1987) defined the vermiculatus Group as: comprising species of moderate-sized individuals with vomerine teeth absent, nuptial pad absent, cutaneus pectoris absent, geniohyoideus lateralis externis inserts on hyoid plate and posterolateral process, and ova half pigmented. Vomerine teeth absent (present but very reduced in *Philautus poecilus*).

Seven specimens collected on south side of Mt. Hilonghilong in northeastern Mindanao Island represent an undescribed species of *Philautus*. They are from montane forest (1600–1700 m). Based on the general slender appearance and absence of the cutaneous pectoral muscle, we have tentatively placed this species in the *vermiculatus*

Group of Dring (1987). A nuptial pad is present for some males.

***Philautus poecilus* new species**

(Figure 2A)

HOLOTYPE.—CAS 133526, south side of Mt. Hilonghilog, Agusan del Norte Prov., Mindanao I., collected by L. Alcala *et al.*, May 1971.

PARATYPES.—CAS 133524-25, 133532, 133543-44; FMNH 250821 (same general locality as holotype).

DIAGNOSIS.—Differs from other Philippine species of *Philautus* in the following combination of characters: an intermediate-sized species, males 21.4–28.1 mm SVL; cutaneous pectoris muscle absent; usually more mottled, ivory-tan and blackish-brown, dorsal pattern (two of seven with dark cruciform mark); small web at base of fingers; SnL 28–34% of HB; TD 23–38% of ED; and lack of dorsal tubercles other than one on eyelid.

DESCRIPTION.—Body moderately tapered from widest part of head to groin; SVL 21.4–28.1 mm for seven males; head broadest at angle of jaws, HB 105–118% of HL and 38–41% of SVL; snout rounded to round-pointed, SnL 28–34% of HB and 33–40% of HL; eye relatively small, ED 73–89% of SnL and 28–32% of HB; tympanum distinct but covered by skin, small, TD 23–38% of ED; snout moderately projecting; nostril much closer to tip of snout than eye; vomerine teeth in very small, low patches for three specimens, absent for one (CAS 133530); vocal sacs present in males; canthus rounded; lores slightly oblique and slightly concave; cutaneous pectoris muscle absent; fingers without webs or with small web at base; disk of third finger largest, its diameter 21–36% of third finger length and 111–200% of TD; subarticular tubercles large (except for basal one on third finger), round, low; palmar area wrinkled; inner metacarpal tubercle elongate; low fringe of skin distally on outer edge of hand; tubercles on outer edge of lower arm variable; nuptial pads not evident for any of the males; hindlimbs long, SVL 58–61% of hindlimb length, TL 50–57% of SVL; toes webbed: to center or distal edge of tubercle for first, to distal edge or slightly beyond on inside of second, third, and fifth, to basal tubercle for fourth; disks of toes smaller than those of fingers; diameter of third toe disk 64–80% of diameter of third finger disk; plantar surface with few, small tubercles; inner metatarsal tubercle elongate, outer lacking; skin of dorsum shagreened without tubercles, except

for very small one on eyelid; belly, under surface of head, throat and proximal part of thighs coarsely granular.

COLOR.—In preservative, dorsum and lateral surfaces mottled blackish brown and ivory tan, occasionally nearly uniform grayish tan with a few dark blotches or a dark cruciform pattern; belly ivory to dusky ivory; under surface of head and throat similar but variously flecked or spotted with brown; hindlimbs with irregular dark and pale transverse bands.

In life, dorsal ground color brownish slate, lightly to heavily mottled with ivory to creamy blotches; lateral surfaces and limbs predominantly ivory colored but with some brownish slate markings.

REPRODUCTION.—No information is available for this species.

ETYMOLOGY.—The name *poecilus* is based on the Greek word *poikilas* meaning mottled.

COMPARISONS.—*Philautus poecilus* differs from other Philippine *Philautus* in the absence of the cutaneous pectoris muscle and nuptial pad, and for this reason it was assigned to the *vermiculatus* Group. It also differs in the more mottled color pattern frequently evident. Based on SVL of adult males (Table 2), it is somewhat larger than the four Philippine species of the *aurifasciatus* Group and somewhat smaller than *P. emembranatus* and *P. surdus* in the *surdus* Group. The minute web at the base of the fingers further distinguishes it from the species of the *aurifasciatus* Group. The tubercle-free dorsum also distinguishes it from *P. longicrus*, *P. schmackeri*, and *P. surdus*.

HABITAT.—The seven known specimens are from montane (moss) forest on Mt. Hilonghilog in northeastern Mindanao Island at an elevation of 1600–1900 meters. Six are from leaf axils of tree *Pandanus* and one from a bird's nest fern. The heights of these sites above the ground ranged from 4–8 m.

RANGE.—Known only from the type locality, Mindanao Island.

**SURDUS GROUP**

Dring (1987) defined the *surdus* Group as: comprising species with small-sized individuals with vomerine teeth present; nuptial pad large, smooth (absent for species of this group other than *surdus*, Liem 1970); cutaneous pectoris present; geniohyoideus lateralis externus inserts on hyoid plate and posterolateral process; and ova unpigmented. The species of this group are ac-

tually moderate-sized, based on Dring's interpretation of moderate for the *vermiculatus* Group (maximum SVL for males of the four species 27.1–33.6 mm). Maximum SVL for males of the three species referred to the *surdus* Group is 27.6–32.4 mm.

### *Philautus emembranatus* (Inger)

*Rhacophorus emembranatus* Inger 1954, 33:392 (type loc., Mount McKinley, Davao Prov., Mindanao Island; holotype in FMNH).

Inger (1954) described *emembranatus* on the basis of a unique, female specimen from the mountains of south-central Mindanao Island. To the best of our knowledge no other examples of this species have been recorded from that area. However, a small series from Mt. Hilonghilog in northeastern Mindanao and from Dapitan Peak, Zamboanga Peninsula, Mindanao, are in close agreement with the type and provide us with some information on the variability for this species and a better understanding of how it differs from other species of the *surdus* Group.

**DESCRIPTION.**—SVL 30.9–43.9 mm for eight females (one measuring 29 mm is not fully mature); 25.1–32.4 mm for seven males; head broadest at angle of jaws; HB 103–122% of HL and 37–46% of SVL; snout round-pointed or ending in a knob-like protrusion, most prominent for several large females, (similar to that exhibited by *Rhacophorus appendiculatus*); SnL 30–35% of HB and 34–41% of HL; eye large; ED 80–97% of SnL and 25–31% of HB; tympanum covered by skin, TD 18–33% of ED; nostril much closer to tip of snout than eye; males with vocal sacs; vomerine teeth reduced to small, low, widely separated patches (absent in one example); canthus rounded; lores moderately oblique, slightly concave; fingers with small web at base; disk of third finger largest, its diameter 22–36% of third finger length, and 133–244% of TD; subarticular tubercles, large low, rounded; no supernumerary tubercles but palm wrinkled; inner metacarpal tubercle elongate, outer indistinct; narrow ridge of flesh on outer edge of fourth finger; outer edge of lower arm smooth or nearly so; nuptial pad large, elongate, smooth; SVL 53–63% of hindlimb length; TL 50–64% of SVL; toes webbed: to approximately distal edge of tubercle or somewhat beyond on inside of first, second, third, and fifth, between penultimate and distal tubercles on fourth (Fig. 4A); diameter of third

toe disk 65–86% of diameter of third finger disk; subarticular tubercles low, rounded; inner metatarsal tubercle elongate; outer indistinct; skin of dorsum lightly shagreened; tubercles usually absent; venter and lower surface of thighs with moderate to large flattish granules.

**COLOR.**—In preservative, dorsum and upper lateral surfaces gray to dusky tan or golden brown, nearly uniform or occasionally with vague, darker blotches; venter creamy white, uniform except for dark flecks along edge of lower jaw and for some individuals a few on posterior abdomen and under-surface of thighs; limbs without distinct transverse bands.

In life, dorsal ground color tannish brown, slate-gray, or dark brown, usually relatively uniform or with a few scattered, darker markings.

**REPRODUCTION.**—The ovaries of the largest female (CAS 183415) held 22 large (2.25 mm), uniform creamy-white eggs. Deposition site and developmental stages have not been observed.

**COMPARISONS.**—This is one of three Philippine species placed in the *surdus* Group (Dring, 1987). It is the largest species of the group. It differs from the other species in: the more uniform coloring of the dorsum; the absence of tubercles on the dorsal surfaces and limbs; the small eye, as a ratio of ED/HB; the small tympanum, as a ratio of TD/ED; and the less dilated toe disks, as a ratio of diameter of third toe disk over diameter of third finger disk (Table 2). Three examples from a population on Mt. Kitanglad, Mindanao are tentatively assigned to this species. The skin is smoother than is typical of the species.

**HABITAT.**—Specimens are from submontane and montane forest, between 800–2100 m elevation.

**RANGE.**—Recorded from mountain ranges in Agusan del Norte, Davao, Misamis Occidental, and Zamboanga del Norte Provinces, Mindanao Island.

### *Philautus surdus* (Peters)

*Polypedates surdus* Peters, 1863:459 (type loc.: Luzon Island; holotype in ZMB).

*Philautus williamsi* Taylor, 1922:167 (type loc.: Polillo Island; holotype in Philippine Bureau of Science, destroyed during World War II).

*Rhacophorus lissobranchius* Inger, 1954:390 (type loc.: Mount McKinley, Davao Prov., Mindanao Island; holotype in FMNH).

Peters (1863) described *Polypedates surdus* on the basis of a unique specimen from Luzon Is-

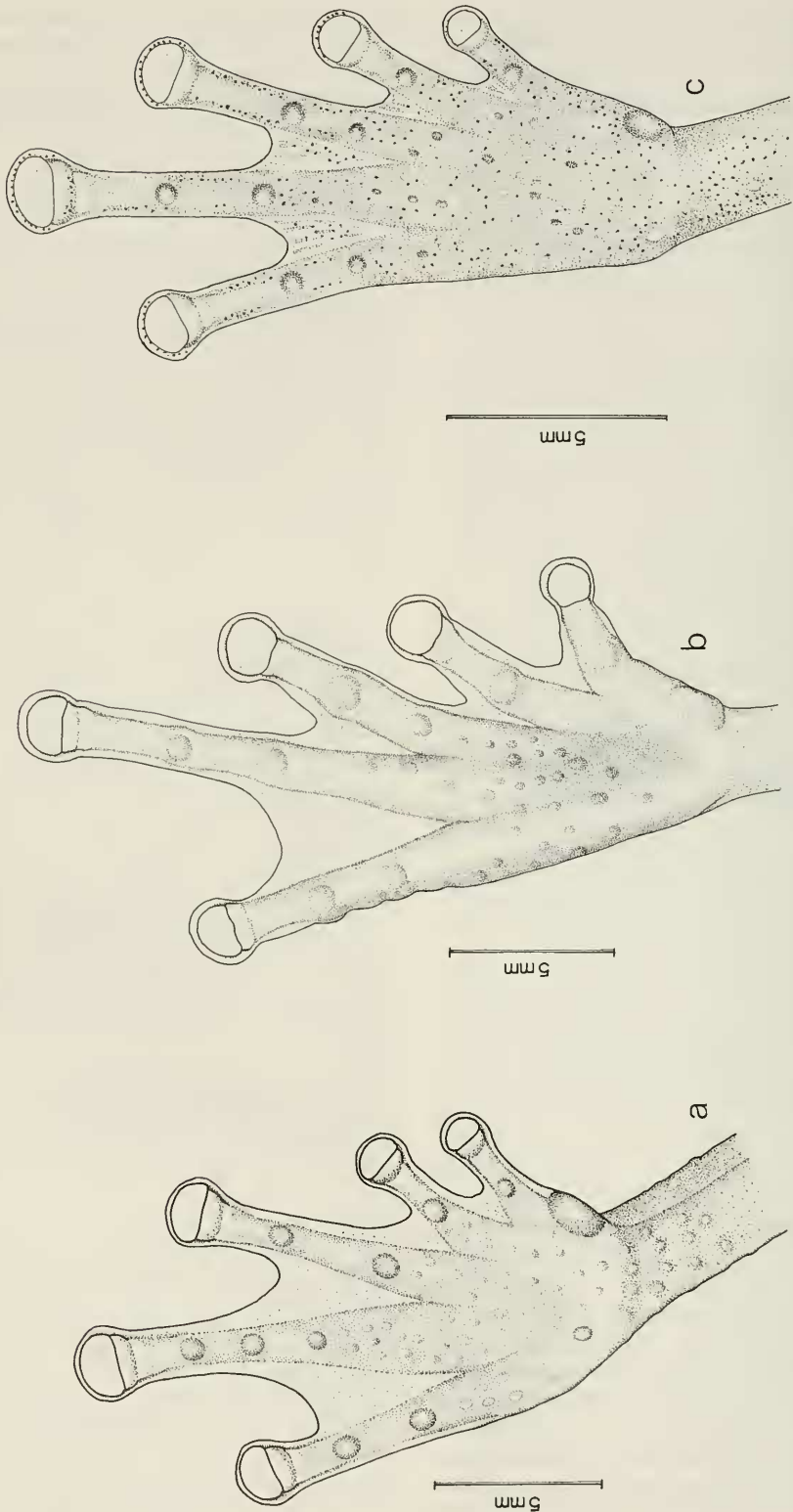


FIGURE 4. Ventral surface of foot, showing extent of webbing and tubercles: (a) *Philautus emembranatus*; (b) *Philautus surdus*; (c) *Philautus surrufus*.

land. Taylor (1920) continued to recognize the species as a polypedatid. In 1922 he collected a series of specimens from Mt. Maquiling, Luzon that he identified as *Rhacophorus surdus*. He did not publish this information and presumably did not compare the specimens with those that he described as *P. williamsi*.

Inger (1954) described *Rhacophorus lissobranchius* on the basis of a single female specimen from Davao Province, Mindanao Island. He noted that the *lissobranchius* resembled *surdus*, following comparison with Taylor's series of that species from Mt. Maquiling. He stated that *lissobranchius* differed in the following characters: snout less projecting, more extensive webbing of fingers and toes, and larger areas of brown on the posterior surfaces of the thighs.

A series of about 50 specimens from the mountains of northeastern Mindanao as well as northwestern Mindanao and Bohol Island are examples of the species represented by the unique type of *lissobranchius*. The variation exhibited by our series for the characters noted above as well as other characters overlap the variation exhibited by the series of *surdus* from Luzon, although the mean extent of the webbing of the toes appears to be greater for populations on the southern islands than on Luzon. Because we cannot demonstrate any other clear differences in the character states for any of the characters we have used, we regard these populations from Luzon, Bohol, and Mindanao as conspecific. We also predict that exploration of suitable microhabitats in the mountain forests in Leyte and Samar will reveal populations of *surdus* on those islands.

Taylor (1920) described *Philautus williamsi*, based on four examples from southern Polillo Island and one from Mauban, Tayabas on the east coast of Luzon. Part of the series, including the holotype, deposited in the Philippine Bureau of Science, were destroyed during World War II. We have compared the remaining paratypes (MCZ 14473 and CAS 62254) with the holotype and a series of *Philautus surdus* from Luzon. Although the examples of *williamsi* are apparently immature, they are in close agreement with the series of *surdus* in terms of webbing of the toes, the pair of tubercles on the dorsum at the shoulder level, the proportional characters used, and the color pattern. We regard these populations as conspecific.

**DESCRIPTION.**—SVL 22.5–31.0 for 25 males and 28.5–38.4 for 20 females (The holotype at

25.2 mm SVL and lacking vocal slits is assumed to be an immature female); head broadest at angle of jaws; HB 107–120% of HL and 39–45% of SVL; snout rounded to round-pointed, occasionally strongly projected (particularly for some larger individuals), SnL 30–40% of HB and 33–43% HL; eye large, ED 86–103% of SnL and 30–37% of HB; tympanum distinct but covered by skin, strong supratympanic fold, TD 33–49% of ED; upper jaw projecting slightly beyond lower jaw (strongly in a few large individuals); nostril closer to tip of snout than eye; vomerine teeth in small, low patches of only a few teeth (occasionally absent or prominent, CAS-SU 20356); vocal sacs present in males; canthus rounded; lores moderately oblique, slightly concave; cutaneous pectoris muscle present but thin; fingers not conspicuously webbed, no more than result of joining of marginal flanges of skin of fingers; diameter of third finger disk 36–45% of third finger length and 111–192% of TD; subarticular tubercles (except for basal one on third finger) large, round, low; palmar area with folds; nuptial pad large, smooth, elongate; SVL 55–69% of hindlimb length and TL 48–60% of SVL; toes webbed: to distal edge of tubercle or somewhat beyond on inside of first and second, nearly to disk for third and fifth toes, and to penultimate tubercle or beyond on fourth toe (Fig. 4B); diameter of third toe disk 83–100% of diameter of third finger disk; subarticular tubercles rounded; supernumerary tubercles elongate inner metatarsal tubercle; outer indistinct; skin of dorsum shagreened, nearly always with a very distinct dorsolateral tubercle at shoulder level on either side (22 in a sample of 30), and usually other scattered tubercles including one or more on upper eyelid, especially for juveniles and males; under surface of head and throat granular for males, less so for females; belly and proximal portion of thighs coarsely granular.

**COLOR.**—In preservative, dorsal ground color from tan to dark, rusty brown (rarely grayish-brown), nearly uniform or with a few darker spots (one pair usually prominently enclosing the pair of shoulder tubercles) or with prominent dark interorbital bar and/or large, dark blotch on body; venter and lower lateral surfaces creamy, lightly to heavily spotted with brown; hindlimbs usually with two or three dark cross-bands; anterior and posterior surfaces of thighs with vague to conspicuous, rusty colored areas; upper lip usually with a vague to prominent pale bar (of varying

width) slanting posteriorly from eye toward or to margin of upper lip.

In life, dorsal ground color grayish or slate-brown to dark brown, usually with some darker spots; hindlimbs usually with dark crossbars.

**REPRODUCTION.**—Several batches of frog embryos and larvae are from the leaf axils of *Pandanus* and the base of arboreal bird's-nest ferns in original forest at elevations of 1200–1500 m on Mt. Hilonghilog (Alcala and Brown 1982). These batches range in number from 5 to 19. Based on the narrow range of developmental stages exhibited by each batch at the time of collection, each batch probably consists of a single clutch. Several batches were allowed to continue development by placing them in plastic bags surrounded by moist root-mass material from aerial ferns. In two instances the fully metamorphosed froglets resulting from this direct development were identified as *Philautus lissobranchius* (now *P. surdus*). This identification is based on color pattern, rugosity of dorsum, toe structure, and extent of webbing of the toes. The estimated developmental time is 38 to 41 days. For details on developmental stages see Alcala and Brown (1982).

**COMPARISONS.**—See *Philautus surrufus* and *P. emembranatus*.

**HABITAT.**—Specimens from Bohol and Mindanao Islands are primarily from dipterocarp to montane forest at elevations from 500–2000 m (rarely below about 650 m).

**RANGE.**—Bohol, Mindanao, Luzon, and Polillo islands.

### *Philautus surrufus* new species

(Figure 2B)

*Rhacophorus surdus* (part): Rabor and Alcala 1959:340.

Brown and Alcala (1970b) referred the specimens in a large collection of *Philautus* from Dapitan Peak, northwestern Mindanao, to four species: *P. acutirostris*, *Rhacophorus* (= *Philautus*) *emembranatus*, *lissobranchius*, and *surdus*. Those referred to *surdus* actually represent a previously undescribed species.

**HOLOTYPE.**—CAS-SU 21013, a female, collected in submontane forest (1800–1900 m) on the west side of Dapitan Peak, about 10 km SE of Masawan, Misamis Occidental Prov., Mindanao Island, by Angel Alcala *et al.*, April 14, 1959.

**PARATYPES.**—Mindanao Island, Zamboanga

del Norte Prov., west side of Dapitan Peak, six to eight km SE Buena Suerte; CAS-SU 20920, 21189–91; Mt. Malindang: FMNH 96043–44; Misamis Occidental Prov., west side of Dapitan Peak, about 12 km E of Masawan: CAS-SU 20955–60; about six to ten km SE of Masawan: CAS-SU 20952, 20962–74, 20976–89, 20995–99, 21023–60, 21062–68, 21070–89, 21092–126, 21145–53, 21156–74, 21181–82, 21194–95, 21658–63, 21667–68, 21670–76; 14 to 15 km SE of Buena Suerte: CAS-SU 20336, 20367, 20375, 20942, 20946–48, 20950–51, 20975, 21183–84, 21654.

**DIAGNOSIS.**—Differs from other Philippine species of the *surdus* Group of *Philautus* in the following combination of character states: the somewhat smaller size, a reddish dorsal color pattern, the reduced webbing between the toes, and the relatively smooth skin.

**DESCRIPTION.**—SVL 20.0–27.6 mm for 16 males and 26.6–35.4 mm for 14 females; head broadest at angle of jaws, HB 104–119% of HL and 40–47% of SVL; snout rounded to round pointed, SnL 32–39% of HB and 33–43% of HL; eye large, ED 92–110% of SnL and 31–39% of HB; tympanum distinct but covered by skin, strong supratympanic fold; TD 34–50% of ED; snout projecting moderately; nostril closer to tip of snout than eye; vomerine teeth in small, low, widely separated patches of only a few teeth; vocal sacs present in males; canthus rounded; lores slightly oblique and slightly concave; cutaneous pectoris muscle present but small; fingers not or barely webbed at base; nuptial pad not discernable for sample of 12 males; diameter of third finger disk 34–44% of third finger length and 106–150% of TD; subarticular tubercles large (except for basal one on third finger), rounded; palmar area with some supernumerary tubercles; inner and outer metacarpal tubercles elongate; SVL 56–64% of hindlimb length and TL 52–61% of SVL; toes webbed: usually to distal edge of tubercle on inside of first, second, third, and fifth; to or nearly to penultimate tubercle on fourth (Fig. 4C); disks of toes usually smaller than those of fingers; diameter of third toe disk 81–96% of that of third finger disk; plantar area with small, scattered tubercles; inner metatarsal tubercle elongate; outer lacking; skin of dorsum finely shagreened, tubercles on dorsum absent even on eyelids or very rarely a few; belly and basal part of posterior surface of thighs covered with large, flattish granules; those under head and throat usually smaller



or area simply more wrinkled; outer edge of hand with low flange of skin or tubercles; outer edge of lower arm usually with few, low tubercles; prominent whitish tubercles are usually present on the outer edge of the foot.

**COLOR.**—In preservative, dorsum and upper lateral surfaces pale to dark reddish-brown nearly uniform for some specimens, with scattered reddish-brown flecks or vague spots, or mottled reddish and tan; occasionally specimens are more pale, grayish to tannish with a few large, reddish-brown blotches. Dark crossbands on hindlimbs are most clearly evident for some of the paler specimens. A rusty-red band occurs on the posterior surface of the thighs, and sometimes there is a less conspicuous band on the anterior surface. The venter is dirty cream or ivory with few to numerous darker (usually brown) flecks or blotches, most concentrated under the head and throat. Some juveniles lack the dark flecks or spots on the venter.

In life, dorsum usually light brown, sometimes limited to the middle region, being darker (blackish) dorsolaterally, and a reddish blush over the light brown region for many examples; hind limbs with dark transverse bars; and sometimes a dark interorbital bar.

**REPRODUCTION.**—Several gravid females have 12–22 large, unpigmented eggs in the ovaries. Deposition site and development are unknown.

**COMPARISONS.**—*Philautus surrufus* differs from *P. emembranatus* in: its smaller size, larger eye relative to HB, larger tympanum relative to eye, larger third finger disk relative to third finger length (Table 2), and some features of the color pattern. It differs from *P. surdus* in: the somewhat smaller size, (most evident for males, Table 2); the smoother, less tuberculate dorsum; and some features of the color pattern. It differs from both species in the less extensive webbing of the toes (Figs. 4A, B, and C).

**HABITAT.**—This species was found at elevations ranging from 800 m in upper dipterocarp forest to about 2300 m in montane (moss) forest. It was most abundant at elevations above 1600 m.

**RANGE.**—Recorded thus far from Mt. Malindang, Dapitan Peak area in northwestern Mindanao Island.

### *Philautus alticola* Ahl

*Philautus montanus* Taylor, 1920:305 (type loc.: Bongao Island, Sulu Archipelago; holotype in Philippine Bureau of Science destroyed during World War II).

*Philautus alticola* can only be evaluated on the basis of Taylor's original description (Taylor 1920) and those of later authors (Ahl 1931; Inger 1954), because the unique holotype in the Philippine Bureau of Science was destroyed during World War II.

**DESCRIPTION.**—Based on those of Taylor and Inger, SVL 39 mm for the unique male; HB 93% of HL and 36% of SVL; snout round-pointed, SnL 50% of HB and 47% of HL; ED 84% of SnL and 42% of HB; a weak supratympanic fold, TD 54% of ED; canthus rounded; lores oblique, slightly concave; fingers webbed at base; diameter of third finger disk 78% of TD; indistinct fold of skin on outer edge of fourth finger and on outside of lower arm; large nuptial pad on first finger; SVL 60% of hindlimb length; TL 56% of SVL; toes webbed: to disk on outside of second toe, otherwise about two thirds webbed; subarticular tubercles well developed; small, conical inner metatarsal tubercle; no fold on outer edge of fifth toe or foot.

**COLOR.**—In life, dorsum uniform lavender-gray, with numerous, small, poorly outlined, yellow spots; lores and upper lip with minute brown dots; creamy yellow spot anterior to and below tympanum; dark spots along sides; venter dusky white to cream, with small dusky spots on chin and larger spots in belly area; anal region dark with light yellow border; hindlimbs transversely barred.

**COMPARISONS.**—Taylor (1920) suggested that the closest relative might be *P. vittiger* from Java; Inger (1954) noted that Taylor's description could just as easily justify a relationship with *P. acutirostris*, *leitensis*, or *petersi*. The size, however, SVL 39 mm for a male (Taylor mentions a large nuptial pad on the first finger) is much greater than the maximum (24 mm) for males of *acutirostris*, *leitensis*, or *petersi*. In fact, it is greater than that recorded for the otherwise largest Philippine species, *Philautus emembranatus*, with a maximum SVL of about 33 mm for males. Actually, the size (SVL 39 mm for the unique male), the proportions SnL/HB, ED/HB, TD/ED, and 3FD/TD (based on measurements in Taylor's original description), head less broad than long, color pattern, general appearance (See Plate 3, Fig. 5, Taylor 1920), and habitat suggest to us that Taylor may have erroneously based his description of *Philautus montanus* on a specimen of *Polypedates macrotis*. We hesitate to refer this species to the synonymy of *macrotis*, however,

until the presence of *macrotis* on Bongao Island is confirmed.

REPRODUCTION.—Data are not available for this species.

HABITAT.—Taylor commented that the specimen was found in a small pool near the summit of Bongao Peak (700 m), Bongao Island.

RANGE.—Bongao Island, Sulu Archipelago.

SPECIMENS EXAMINED.—None.

**Polypedates Tschudi**

*Polypedates* Tschudi, 1838:75. Type species *Hyla leucomystax* Gravenhorst, 1829:26.

*Elophila* Duméril and Bibron, 1841:517.

*Trachykyas* Fitzinger, 1843:31. Type species by original designation: *Polypedates rugosus* Duméril and Bibron, 1841.

DIAGNOSIS.—Size moderate to large (SVL at maturity 40–90 mm for Philippine species); skin of dorsal surfaces smooth or shagreened, usually with some ossification with skull; disks of fingers and toes dilated, completely circumscribed by groove; fingers webbed only at base (*P. eques* an exception); toe disks smaller than those of fingers; toes webbed almost to disks except for fourth toe (for Philippine species); hindlimbs long; anal ornamentation prominent but other dermal ornamentation usually absent; vomerine teeth present; vocal sacs present in some species, absent in others; neuropophysis of eighth vertebra attached dorsolaterally on centrum; terminal phalanges Y-shaped; omosternum slightly forked at base; HB less than HL for Philippine species; Wolffian ducts convoluted; petrohyoideus posterior muscle three slips; eggs small, without pigment (clutch size 150–400 for Philippine species), and deposited in foam nests on vegetation near quiet water pools; feeding larvae are ovoid and robust (Inger 1985b).

KEY TO PHILIPPINE SPECIES OF  
*POLYPEDATES*

- 1a. Males without vocal sacs; dorsum uniform or with two vague, broad, dark, longitudinal stripes ..... 2
- 1b. Males with vocal sacs; dorsum usually with four prominent, dark longitudinal stripes (rarely uniform) ..... *P. leucomystax*
- 2a. Usually dark brown stripe from eye through tympanum to axilla or beyond; skin of head usually involved in ossification in frontoparietal area; two promi-

nent whitish tubercles below vent .....  
..... *P. macrotis*

- 2b. No dark brown stripe on side of head; skin of head free of ossification; two prominent whitish tubercles above vent ..... *P. hecticus*

**Polypedates hecticus (Peters)**

*Polypedates hecticus* Peters, 1863:457 (type loc.: Loquilocum, Samar Island; holotype lost).

This species was based on a single example from Samar Island. Günther (in litt., October, 1991) states that the holotype cannot be found in the collections at the ZMB. It is further unlikely that the holotype of *P. hecticus* was ever transferred to any other institution, because the holotype (ZMB 4920) of *P. surdus* from Luzon, which Peters described in the same short paper in 1863, is there. The specimen, furthermore, was examined by Wolf prior to publication of his revision of the genus *Rhacophorus* (1936). Wolf retained the species, indicating that he regarded it as being closely related to *P. leucomystax*. Inger (1954) also retained *hecticus* as a valid species of *Rhacophorus*. In view of the fact that the herpetofauna of Samar and its small satellite islands has not been surveyed extensively and is poorly represented in collections, we follow Wolf and Inger in retaining *hecticus* as a possible valid species. However, based on Wolf's opinion as to relationships and the narrow head relative to length, we tentatively assign *hecticus* to the genus *Polypedates* to which *leucomystax* and *macrotis* (includes *linki*) are already assigned.

DESCRIPTION.—Based on the descriptions of Peters, Ahl, Wolf, and Inger: SVL 51 mm for one male (Ahl 1931); HB 82% of HL and 33% of SVL; snout truncated, projecting; ED about equal to SnL; tympanum distinct; TD about two thirds of ED; canthus acute; lores vertical, concave; vomerine teeth in two small, oblique patches; males without vocal sacs; fingers webbed at base; diameter of first finger disk about half of TD; subarticular tubercles weakly developed; SVL 61% of hindlimb length; TL more than one half SVL; toes, except the fourth, webbed almost completely; toe disks similar to finger disks; subarticular tubercles large; inner metatarsal tubercle elongate; skin of dorsum granular; a distinct dorsolateral fold beginning at eye; belly and undersurface of thighs granular; two enlarged, whitish tubercles above vent.

**COLOR.**—In preservative, dorsal ground color grayish blue; dorsolateral fold whitish, bordered by black; white line from tip of snout along upper lip, widening in front of tympanum; dark flecks in the temporal region, anterior and posterior to tympanum; light blue with blackish flecks on sides; limbs brownish with more or less distinct flecks, particularly on posterior surface of legs; venter whitish.

**COMPARISONS.**—Wolf (1936) indicated a close relationship to *P. leucomystax linki*. Absence of vocal sacs, if verified, is in agreement with *P. macrotis* as opposed to *P. l. leucomystax* for this character state. Based on the unique example and Peter's description, it would appear to differ from *P. macrotis* in some features of the color pattern, the slightly narrower head, and shorter hindlimbs.

**REPRODUCTION.**—No information is available for this species.

**HABITAT.**—Unknown.

**RANGE.**—Known only from the type locality, Samar Island.

**MATERIAL EXAMINED.**—None.

### **Polypedates leucomystax leucomystax** (Gravenhorst)

*Hyla leucomystax* Gravenhorst, 1829:26 (type loc.: Java; syntypes in Breslau Mus., according to Stejneger 1907).

*Hyla sexvirgata* Gravenhorst, 1829:28 (type loc.: Java; holotype in Breslau Mus., according to Stejneger 1907).

*Hyla quadrilineata* Weigman, 1835:260 (type loc.: Manila, Luzon Island, Philippines; holotype disposition unknown).

*Polypedates rugosus* Duméril and Bibron, 1841:520 (type loc.: Java and Manila, Luzon Island; syntypes in MNHN).

*Polypedates megacephalus* Hallowell, 1860:507 (type loc.: Hong Kong; holotype in ANSP).

*Hylarana longipes* Fischer, 1885:47 (type loc.: Pagat, Borneo; holotype in BMNH).

*Rhacophorus braueri* Vogt, 1911:180 (type loc.: Formosa; holotype in ZMB).

Bartlett (1894) was the first to note that both the striped and unstriped color patterns occurred in some Bornean populations. He, therefore, placed *Rhacophorus quadrilineata* in the synonymy of *Rhacophorus leucomystax*.

**DESCRIPTION.**—SVL 49.7–56.6 mm for males and 57.5–75.2 mm for 15 females (one at 59 mm was, however, immature); HB 89–100% of HL and 31–38% of SVL; snout round pointed, SnL 41–48% of HB and 40–45% of HL; eye moderate, ED 61–80% of SnL and 27–38% of HB; tympanum large, TD 64–88% of ED; canthus sharply rounded; lores moderately oblique to nearly ver-

tical, not or shallowly concave; fingers with basal webs between first and second and second and third; diameter of third finger disk 27–33% of third finger length and 52–82% of TD; subarticular tubercles large, elongate; supernumerary tubercles present; inner metacarpal tubercle elongate; outer, small, rounded; hind limbs long, SVL 57–67% of hind limb length and TL 49–55% of SVL; toes webbed: between tubercle and disk for first, second, third, and fifth toes, and to distal tubercle on fourth; diameter of third toe disk 57–78% of diameter of third finger disk; subarticular tubercles large, pointed distally; inner metatarsal tubercle large, oval; outer absent or very small; skin of dorsum smooth or nearly so; skin of head partially ossified with skull for adults; venter coarsely granular except beneath head and throat which is smooth to finely granular.

**COLOR.**—In preservative, dorsal ground color grayish to grayish-tan or brown, with four vague to conspicuous, narrow, dark, longitudinal stripes (sometimes broken or incomplete), occasionally only with dark spots; usually a narrow brownish band on the upper half of the lores and between the eye and forelimb; limbs with dark, transverse bars; venter ivory-white, with or without dark spots on chin and throat.

In life, dorsal ground color grayish or yellowish green to green or brownish, usually with four dark, longitudinal stripes or rows of spots (occasionally uniform); hindlimbs with dark transverse bars.

**REPRODUCTION.**—On Negros *Polypedates leucomystax* breeds from April to December, the rainy months (Alcala 1982). The foamy egg masses of this species occur on leaves of trees, shrubs, or grasses overhanging isolated pools and ponds or quiet pools of temporary streams. Occasionally the masses occur on rocks on the banks of such pools. The egg masses have 150–225 eggs or embryos. Nests with as many as 800–900 eggs have been reported by Taylor (1921) and Villadolid and del Rosario (1930). Larvae break free from the foam-mass and fall or wriggle into the water two to three days after deposition (Alcala 1962). For a discussion of the habits of the free swimming larvae and a description of developmental stages, see Alcala (1962).

**COMPARISONS.**—See comparisons under *Polypedates macrotis*. As to geographic variation among populations of *P. l. leucomystax*, Inger (1966) notes that the spotted pattern on the dor-

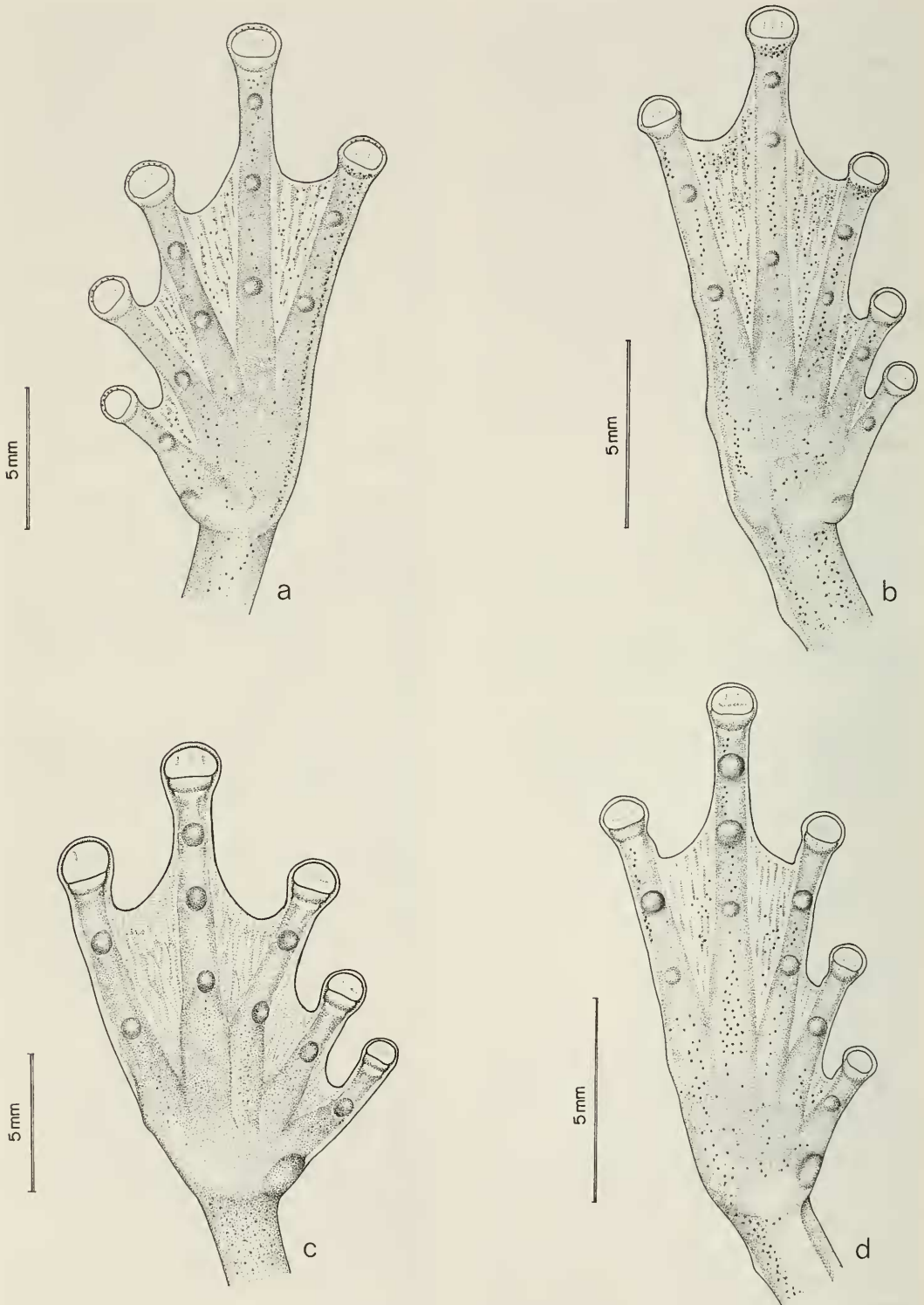


FIGURE 5. Ventral surface of foot, showing extent of webbing and tubercles: (a) *Polypedates macrotis*; (b) *Rhacophorus appendiculatus*; (c) *Rhacophorus bimaculatus*; (d) *Rhacophorus everetti*.

sum is more frequent in Javan and Sumatran populations than in Bornean and Philippine populations, and that samples of males from Philippine, Bornean, Javan, and Sumatran populations exhibit some significant differences in body proportions when measurements such as head breadth, third-finger disk diameter, or tympanum diameter are expressed as ratios of SVL.

**HABITAT.**—This species occupies a wide range of habitats including lowland forest and most man-controlled lowland cultivated areas (Brown and Alcalá 1964, Inger 1966).

**RANGE.**—India; Taiwan; northern Indochina to Borneo, Sulawesi, and the Philippines where it is found on many of the small as well as large islands.

### *Polypedates macrotis* (Boulenger)

*Rhacophorus macrotis* Boulenger, 1891:282 (type loc.: Baram district, Sarawak, Borneo; holotype in BMNH).

*Polypedates linki* Taylor, 1922b:276 (type loc.: Jolo Island, Philippines; holotype in CAS).

**DESCRIPTION.**—SVL 34.8–46.7 mm for 16 mature males and 59.9–71.3 mm for six mature females; HB 89–103% of HL and 30–34% of SVL; snout rounded as viewed ventrally; SnL 38–46% of HL and 42–48% of HB; eye large, Ed 71–92% of SnL and 32–41% of HB; supratympanic fold encroaching on tympanum dorsally; TD 50–75% of ED (one of eight greater than 66%); canthus sharply rounded; lores slightly concave, oblique; vomerine teeth in oblique rows from anterior edge of choanae; males lack vocal sacs; fingers webbed at base; diameter of third finger disk 25–34% of third finger length and 56–93% of TD; subarticular tubercles rounded; supernumerary tubercles present; inner metacarpal tubercle elongate; SVL 58–68% of hindlimb length; TL 51–58% of SVL; toes webbed: almost to disk on inside of first, second, third, and fifth, and beyond penultimate tubercle for fourth (Fig. 5A); diameter of third toe disk 64–85% of third finger disk; subarticular tubercles rounded; no inner metatarsal tubercle present, outer usually absent; skin of dorsum nearly smooth; low whitish ridge on outer forearm; underside of head and posterior to axillary region smooth; belly and posterior surface of thighs coarsely granular; dark colored patch around vent usually bordered by two prominent white tubercles below and occasionally by conspicuous whitish granules above.

**COLOR.**—In preservative, dorsal ground color grayish, tan or medium brown, usually with few

to numerous small, darker spots; or two broad, dark, longitudinal stripes, usually a faint to distinct brown band narrowing posteriorly extending from eye to axilla or beyond and covering or partially covering tympanum; limbs with dark cross bars; venter cream to light tan, frequently with brown spots laterally and under head and throat.

**REPRODUCTION.**—Eggs, clutch size 300–400, are deposited in foam nests attached to leaves of shrubs or trees and occasionally grasses above or bordering pools in small streams (Inger 1966, Brown and Alcalá 1983). See Inger (1985b) for a description of larva and larval development.

**COMPARISONS.**—*Polypedates macrotis* is similar to *P. leucomystax* and may be closely related to that species. It differs from *leucomystax* in the absence of vocal sacs, the typical color pattern, the longer hindlimbs relative to snout-vent length, the broader head relative to HL, and size of the tympanum relative to the eye. As noted by Inger (1966), the available sample from the Palawan population indicates a smaller size (SVL) than for members of the Bornean population. The limited sample from the Jolo Island (Sulu Archipelago) population does not permit a similar comparison.

**HABITAT.**—Specimens from Palawan were from banks of streams or ditches at the edge of the forest or in coconut groves at low elevations.

**RANGE.**—Philippines: Palawan I., Busuanga I., Calauit I., Jolo I., Dumaran I., Borneo.

### *Rhacophorus* Kuhl and van Hasselt

*Rhacophorus* Kuhl and van Hasselt, 1822:104. Type species by monotypy: *Rhacophorus moschlatus* Kuhl and van Hasselt, 1822.

*Racophorus* Schlegel, 1826:239. Emendation of *Rhacophorus* Kuhl and van Hasselt, 1822.

*Leptomantis* Peters, 1867:32. Type species by monotypy: *Leptomantis bimaculata* Peters, 1867.

Liem (1970) states that the group of species referred to *Rhacophorus* share a combination of character states that separate them from other genera by definite gaps. He also notes that three species, *R. appendiculatus*, *R. everetti*, and *R. microtympanum* represent a subgroup that differs in several respects from other species assigned to the genus. Two of these three are among the four species occurring in the Philippines.

**DIAGNOSIS.**—Size moderate to large (SVL 30–70 mm at maturity for Philippine species); HB equal to or greater than HL; dermal ornamentation

tation on limbs of some species and around vent; disks of fingers and toes moderate to large, completely circumscribed by groove; finger webbing varying from basal to almost fully webbed; hindlimbs long; vomerine teeth usually present (present in all Philippine species except *R. bimaculatus*); vocal sacs present in males; terminal phlanges Y-shaped; omosternum forked at base; Wolfian ducts convoluted; petrohyoideus posterior muscle three slips; eggs small to moderate, unpigmented; clutch size 50–400 for those species known for this character; eggs deposited in foam nests attached to leaves of trees or shrubs overhanging quiet pools or streams (site unknown for *R. bimaculatus* and *R. gauni*); larvae adapted to quiet pools or, in the case of *R. bimaculatus* and *R. gauni*, to streams with moderate to strong currents (Inger, 1985b).

KEY TO THE PHILIPPINE SPECIES OF  
*RHACOPHORUS*

- 1a. Web between outer fingers reaching distal subarticular tubercle or beyond ..... 2
- 1b. Web between outer fingers not reaching distal subarticular tubercle ..... 3
- 2a. First finger webbed to distal tubercle, other fingers to disk; a flap of skin dorsal to anus; prominent whitish anal tubercles lacking ..... *R. pardalis*
- 2b. Inner fingers webbed only at base; outer fingers to distal tubercle; a small flap of skin may be present dorsal to anus; usually several prominent white tubercles mostly ventral to vent ..... *R. bimaculatus*
- 3a. Fingers webbed beyond basal tubercle, web reaching the distal subarticular tubercle of fourth finger; a dermal flap on either side below the vent ..... *R. appendiculatus*
- 3b. Fingers webbed only at base, web not reaching the distal subarticular tubercle of fourth finger; no dermal flap below vent ..... *R. everetti*

***Rhacophorus appendiculatus* (Günther)**

*Polypedates appendiculatus* Günther, 1859:79 (type loc.: Philippine Islands, syntypes in BMNH).

DESCRIPTION.—SVL 29.3–35.4 mm for 18 males and 41.1–51.5 mm for 8 females; HB 100–111% of HL and 35–39% of SVL; snout protruding, with rounded pale-colored projection, most prominent in females, its length 35–41%

of HL and 36–43% of HB; ED 73–98% of SnL and 36–43% of HB; tympanum exposed with supratympanic fold extending from eye to axilla; TD 43–50% of ED and 100–143% of diameter of third finger disk; canthus rounded; lores oblique, slightly concave; vomerine teeth in oblique rows, shorter than space separating them; males with vocal sacs; fingers about  $\frac{1}{4}$  to  $\frac{1}{3}$  webbed; diameter of third finger disk 25–37% of third finger length and 124–158% of third toe disk; subarticular tubercles rounded; supernumerary tubercles absent; inner, oval metacarpal tubercle, outer absent; whitish ridge along outer edge of fourth finger and lower arm; SVL 59–67% of hindlimb length, TL 48–57% of SVL; toes webbed: almost to disk on inside of second, third, and fifth, about halfway between disk and tubercle on first and almost to distal tubercle on fourth (Fig. 5B); subarticular tubercles rounded; supernumerary tubercles absent; narrow, inner metatarsal tubercle, outer absent; low whitish ridge on outer edge of fifth toe and tarsus, occasionally a small flap of skin at heel; underside of head and anterior to axilla smooth; belly and posterior surface of thighs coarsely granular; transverse, crenulated, whitish, dermal ridge below vent, sometimes divided into two or four sections.

COLOR.—In preservative, dorsum grayish to tan, brown or purplish-brown, nearly uniform to rather heavily blotched; occasionally a distinct dark bar or patch between eyes; usually hindlimbs with dark transverse bars or patches, least evident for Negros population; venter uniformly cream to tan.

In life, dorsum grayish to brown, uniform or with dark blotches; venter pale yellow.

REPRODUCTION.—Clutch size is 300–400 small, unpigmented eggs for a gravid female from the Philippines (Brown and Alcala 1983). The egg-deposition site is unknown, but is probably a foam nest on shrubs or trees adjacent to a quiet body of water. A complete developmental series is not available, but Inger (1966) identifies larvae (stages 36–39) with this species, as do Alcala and Brown (1982) for a larval series (stages 40–44). The latter differ somewhat from those collected by Inger (see Alcala and Brown, 1982), and it is possible that one or both of these larval series have been misidentified.

COMPARISONS.—The four species of *Rhacophorus* occurring in the Philippines are readily distinguished from each other on the basis of:

webbing of the fingers and toes, dermal appendages, and color pattern. The samples of *R. appendiculatus* from various islands in the Philippines do not exhibit any consistent differences for characters studied. As noted by Inger (1966) the Philippine populations of *R. appendiculatus* have less extensive webs between the toes and reduced dermal appendages on the limbs when compared with samples from the Bornean populations.

**HABITAT.**—Nine specimens (all males) from Negros and one from Bohol are from dipterocarp forest at elevations of 300–600 m.

**RANGE.**—Reported from Malay Peninsula, Sumatra, Borneo, and Philippine Islands.

### *Rhacophorus bimaculatus* (Peters)

*Leptomantis bimaculata* Peters, 1867:32 (type loc.: Agusan Valley, Mindanao, Philippines; holotypes in ZMB).

*Philautus zamboangensis* Taylor, 1922:173 (type loc.: Pasonanca, Zamboanga Prov., Mindanao Island; holotype in CAS).

This species was described by Peters (1867) and placed in a new genus *Leptomantis*. Boulenger (1882b) referred the species to the genus *Ixalus*, and Stejneger (1905) to the genus *Philautus*. Assignment to *Philautus* was continued by subsequent authors until 1970, at which time Liem referred the species to the genus *Rhacophorus* based on the combination of characters that he used to define that genus. Dubois (1981) followed Liem in placing the genus *Leptomantis* in the synonymy of *Rhacophorus*. Inger (1985a) retained the species in the genus *Philautus*, apparently inadvertently, because he did not refer to Liem's or Dubois' generic assignment in his comments (1985a:527).

Liem (1970) in transferring the species to *Rhacophorus* stated that the name *bimaculatus* was preoccupied by that of Boulenger (1882b), and the available name was *zamboangensis* of Taylor (1922). In so doing he failed to note that Ahl (1927) had nullified the question of preoccupation in his substitution of the name *bipunctatus* for the species described by Boulenger as *Rhacophorus bimaculatus*. Inger (1985a) noted that Ahl's substitute name (*bipunctatus*) is valid. Thus Peter's *bimaculatus* is the valid name for this species.

**DESCRIPTION.**—SVL 28.3–33.5 mm for 18 males (The holotype, a male, measures about 33.5 mm SVL in its present state of preservation.) and 33.3–40.7 mm for 10 females; HB 102–

111% of HL and 32–37% of SVL; snout short, SnL 32–40% of HB and 36–41% of HL, rounded at level of jaws, truncate at level of nostrils; upper jaw slightly protruding; eye large, ED 87–117% of SnL and 30–41% of HB; tympanum small, TD 31–43% of ED and 63–100% of third finger disk; canthis rounded; lores sloping, occasionally somewhat concave; vomerine teeth lacking; vocal sacs of males opening by long slits; fingers webbed only at base between first and second, to distal edge of basal subarticular tubercle between second and third finger and distal subarticular tubercle on between third and fourth fingers; low supernumerary tubercles sometimes evident close to basal tubercles; finger disks moderately broader than penultimate phalanx, ovoid in shape; disk of third finger largest, diameter of third finger disk 27–36% of third finger length and 117–150% of third toe disk; SVL 54–61% of hindlimb length, TL 53–58% of SVL; disks of toes smaller than those of fingers; toes webbed: beyond distal edge of tubercle on inside of first and third, nearly to disk on inside of second and fifth, and between penultimate and distal tubercles for fourth (Fig. 5C); no supernumerary tubercles; metatarsals smooth; oval inner, but no outer metatarsal tubercle; outer edge of metatarsal area with a low ridge or fold of skin; dorsum smooth; belly with flattish granules; chin and throat not granular, usually a small whitish tubercle dorsal and lateral to vent on each side and several ventral to vent; prominent tubercle at distal end of tibia.

**COLOR.**—In preservative, dorsum pinkish gray to tan-colored, or reddish brown, usually with some small darker spots, occasionally with some large, irregularly shaped, dark blotches and for many specimens a narrow, dark, transverse bar between eyes; hindlimbs usually with vague, light and dark, transverse bars dorsally; ivory or cream-colored bar on spot on upper jaw below eye (absent for only one specimen), and occasionally similar spots on band along margin of upper jaw anterior to eye; under surfaces usually uniformly pale.

In life, dorsum pale orange-brown to carmine-brown to pale reddish lilac, nearly uniform or with darker flecks or blotches; a narrow, dark interorbital bar for Philippine specimens; for Bornean specimens, "sandy or dark brown above, a narrow, dark interorbital bar; three transverse, dark ovals on dorsum, one at occiput, one at the center of the back, and one over the sacrum; top

of snout usually lighter than back; sides of head and body and anterior and posterior faces of thigh blackish brown; a conspicuous white or pink spot below eye; sides of body and anterior and posterior faces of thigh with pale spots (light blue in life); venter white, immaculate or dusted with brown" (Inger 1966).

**REPRODUCTION.**—Gravid females produce about 25–40 relatively large, non-pigmented eggs (Brown and Alcalá 1983). The exact site of egg deposition is not known, but we observed a pair in amplexus on a rock in a stream bed (700 m) and a metamorphosing young on a leafy branch overhanging a stream (1100 m) on the same mountain. Inger (1966) observed another pair in amplexus at the entrance to a hole in a forest stream-bank. Larvae from rocky pools and riffles of mountain streams in northern Borneo are identified with *R. gauni*, a species that is very closely related to *bimaculatus* (Inger and Tan 1990).

**COMPARISONS.**—*Rhacophorus bimaculatus* is not closely related to other species presently recorded from the Philippines, but Liem (1970) and Inger (1985b) consider *R. gauni* from Borneo as closely related. We have not compared samples of the Bornean and Thailand populations referred to *bimaculatus* with samples from Philippine populations to determine to what extent these populations may be differentiated because the Philippines is the type locality. This needs to be done, however, because this forest-restricted frog would not be a likely candidate for frequent dispersal across water.

**HABITAT.**—Philippine specimens range from 400–800 m elevation in dipterocarp forest.

**RANGE.**—Mindanao, Bohol, and Luzon islands of the Philippines, Borneo, and Thailand.

### *Rhacophorus everetti everetti* Boulenger

*Rhacophorus everetti*; Boulenger, 1894:87 (type loc.: Palawan Island; syntypes in BMNH).

**DESCRIPTION.**—SVL 30.0–31.8 mm for 4 males and 35.4–41.4 mm for 4 females; HB 105–117% of HL and 36–42% of SVL; snout bluntly rounded to nearly truncate not projecting much beyond lower jaw, its length 36–38% of HL and 31–35% of HB; eye large, ED 96–115% of SnL and 33–38% of HB; tympanum with supratympanic fold from eye to axilla, TD 34–46% of ED; canthus rounded; lores slightly oblique and concave; vomerine teeth in short, oblique rows; males with

vocal sacs; fingers webbed at base; diameter of third finger disk 27–34% of third finger length and 85–113% of TD disk; subarticular tubercles rounded; supernumerary tubercles prominent; inner metacarpal tubercle present, but no outer; SVL 51–61% of hindlimb length, TL 54–66% of SVL; toes webbed: usually nearly to disk on inside of first, second, third and fifth, and between penultimate and distal tubercles for fourth (Fig. 5D); diameter of third toe disk 65–88% of third finger disk; subarticular tubercles rounded, supernumerary tubercles not distinct; a short inner but no outer metatarsal tubercle; skin of dorsum shagreened; venter with moderate flat granules; posterior surface of thighs smooth; several whitish, conical tubercles below vent; lateral edge of lower arm tarsus and distal end of tibia with whitish tubercles.

**COLOR.**—In preservative, dorsal ground color pinkish-gray or dark ivory to light brown with dark brown interorbital bar, a large, dark brown blotch (with three anterior and two posterior prongs) on body, and numerous scattered, small spots or blotchy; limbs with dark bars and usually small dark spots; venter creamy-white to dusky ivory.

In life, dorsal ground color grayish, tan or light brown, usually with blackish spots or blotches; hindlimbs with dark cross bars.

**REPRODUCTION.**—Clutch sizes of about 30 non-pigmented eggs for one female and 12 large eggs and about the same number of small eggs (possibly not maturing at the same time) from one ovary of another female are known (Brown and Alcalá 1983). This gives a clutch range from 25–50 (the latter, if all were to mature and be deposited at the same time). The egg-deposition site and the mode of reproduction are unknown for this species; but Inger (1954) reports capture of a pair in amplexus on a shrub along a stream bank.

**COMPARISONS.**—*Rhacophorus everetti* is readily distinguished from other Philippine *Rhacophorus* by color pattern, webbing of the toes, and pointed tubercles along the tarsus. Inger (1966) recognized two subspecies, *R. e. everetti* in Palawan and *R. e. macroscelis* in Borneo.

**HABITAT.**—Philippine specimens are from dipterocarp and lower submontane forest at elevations of 350–1000 m. This species occurs at 1800 m in montane forest in northwestern Borneo (Inger and Stuebing 1992).

**RANGE.**—Palawan Island and Borneo.



**Rhacophorus pardalis** Günther

*Rhacophorus pardalis* Günther, 1859:83 (type loc.: Philippines; holotype in BMNH).

*Rhacophorus rizali* Boettger, 1899:1 (type loc.: Dapitan, Mindanao Island; holotype in MTKD).

**DESCRIPTION.**—SVL 40.1–50.7 mm for 10 males and 49.3 (probably mature) to 66 mm for 12 females; HB 100–110% of HL and 32–36% of SVL; snout broadly rounded, nearly truncate at nostril level when viewed dorsally; upper jaw only slightly protruding; its length 38–44% of HL and 34–41% of HB; eye large, ED 78–94% of SnL and 31–37% of HB; tympanum distinct, upper edge bordered by fold extending from eye to axilla; TD 41–59% of ED and 66–100% of third finger disk; canthus rounded; lores oblique, slightly concave; vomerine teeth present, slightly oblique, separated by distance about equal to length; males with vocal sacs; fingers, except first webbed almost to disks; diameter of third finger disk 33–42% of third finger length and 130–170% of third toe disk; subarticular tubercles rounded; supernumerary tubercles absent: inner metacarpal tubercle elongate; outer tubercle absent; SVL 61–69% of hindlimb length, TL 47–54% of SVL; toes webbed almost to disk, except for second and third on outside; toe disks smaller than finger disks; subarticular tubercles rounded supernumerary tubercles absent; metatarsal tubercle elongate; outer absent; a low flange of skin on outer edge of foot; skin of dorsum tubercles; underside of head and throat smooth; belly and posterior surface of thighs with small to moderate granules; usually a fold of skin below vent; more rarely dorsal to vent.

**COLOR.**—In preservative, dorsum grayish-tan, tan, light brown, or reddish brown, usually with some darker, small spots or large blotches; usually a narrow, dark interorbital bar; some specimens with whitish or creamy spots along dorso-lateral surfaces, posterior body and hindlimbs; venter pale ivory to pale tan; occasionally a few dark spots along margin of lower jaw; limbs usually with narrow, dark cross bars.

In life, dorsal ground color pale carmine-brown to brown-lilac, usually with darker purplish blotches and frequently with creamy white blotches dorsolaterally and on hindlimbs for specimens from Negros and Bohol islands; dorsum “bright yellow-green” for examples from a population on Polillo Island (R. Crombie, in litt., October 7, 1992).

**REPRODUCTION.**—On Negros Island, the foamy egg masses of this species occur on leaves of ferns overhanging pools in small, mountain streams in the submontane forest. Another foamy egg mass, floating on the water in a cavity in a dead tree, was also tentatively identified with this species. Eggs are about 3 mm in diameter, non-pigmented, and numbered 44–50 per clutch. Details of development through stage 46 were observed in the laboratory and reported by Alcala (1962). These egg masses were deposited in March, April, and May.

**COMPARISONS.**—*Rhacophorus p. pardalis* is readily distinguished from other species in the Philippines by the more extensive webbing of the hands, reaching to the disk on the second, third, and fourth fingers. The populations on various islands in the Philippines do not exhibit consistent differences for any of the characters studied. Inger (1966) notes that samples from Bornean populations have slightly longer hindlimbs and narrower heads relative to SVL than do samples from Philippine populations.

**HABITAT.**—Specimens from Bohol and Negros range from dipterocarp to montane forests at elevations of 500–1700 m.

**RANGE.**—Philippines, Borneo, and Sumatra.

#### ECOLOGY AND ZOOGEOGRAPHY OF PHILIPPINE RHACOPHORIDS

Recent faunal surveys conducted by the authors on well-forested mountains on Mindanao, Bohol, Mindoro, Palawan, and on a number of smaller, less mountainous islands provide extensive collections of most of the known species of Philippine rhacophorids and data on ranges, elevational distribution, general habitats, microhabitats, and egg-deposition sites. This information and comparable data on Bornean populations of the same species or related species are briefly summarized.

#### OBSERVATIONS ON THE ECOLOGY

*Nyctixalus.*—Both *N. pictus* and *N. spinosus* occur in original (rarely secondary) dipterocarp forest at elevations between 150 and 1100 m. Our observations on these species in the Philippines indicate that they are primarily in the lower vegetation strata (up to one or two meters). Walls of tree holes or similar cavities are the known egg-deposition sites for *N. pictus* and presumably *N. spinosus* (Inger 1966, Alcala and

TABLE 3. Microhabitat distribution patterns of Philippine populations of species of *Philautus* and *Rhacophorus*. Samples and (percentages) are given for five categories of microhabitats.

Species	Total sample	Ferns	<i>Pandanus</i>	Other trees	Shrubs	Forest floor level
<i>Philautus</i>						
<i>acutirostris</i>	90	14 (16)	14 (16)	7 (8)	7 (8)	48 (52)
<i>leitensis</i>	38	6 (16)	7 (18)		6 (16)	19 (50)
<i>longicrus</i>	64		4 (6)		1 (2)	59 (92)
<i>poecilus</i>	7	1 (14)	6 (86)			
<i>schmackeri</i>	232	76 (33)	8 (3)	7 (3)	87 (38)	54 (23)
<i>surdus</i>	58	38 (66)	11 (19)	2 (3)	3 (5)	4 (7)
<i>emembranatus</i>	15	6 (40)	3 (20)	1 (7)	2 (13)	3 (20)
<i>surrufus</i>	77	52 (68)	6 (8)	4 (5)	3 (4)	12 (18)
<i>Rhacophorus</i>						
<i>appendiculatus</i>	10			10 (100)		
<i>bimaculatus</i>	20			8 (40)	8 (40)	4 (20)
<i>everetti</i>	7	1 (14)		1 (14)	1 (14)	4 (57)
<i>pardalis</i>	21		2 (5)	6 (33)	11 (57)	2 (5)

Brown 1982). Larval development takes place in the basins of water in tree holes (Inger 1985b, Alcalá and Brown 1982).

*Philautus*.—Data on zonation and microhabitats in the mountains of the larger islands are available for eight Philippine species of *Philautus*. Most have been recorded from the mid-dipterocarp (300–500 m) through the montane forest that starts between about 800–2000 m, depending on the height of the mountain surveyed. *Philautus poecilus* is known only from the submontane and montane zones. *Philautus longicrus* on Palawan is also recorded in a few instances (eight out of 100 examples) from elevations of 100 m or less in the lower dipterocarp. For Philippine species of *Philautus*, density, based on sample sizes, is higher in the submontane and montane forest zones. This observation is in agreement with the reported zonal distribution of *Philautus* in Bornean forests (Dring 1987). Also, eight of 11 species of *Philautus* from Mt. Kindbalu, Mt. Mulu, Mt. Lumaku, and the Crocker range in northwest Borneo are thus far recorded only from the montane zone, above the dipterocarp zone (Inger and Stuebing 1992). Their “montane zone” includes the submontane zone of many authors.

Our data show that all eight species of *Philautus* occupy microhabitats from the forest floor to leaf-axils and arboreal ferns in the canopy stratum. As summarized in Table 3, the species of *aurifasciatus* and *surdus* Groups are segregated to some degree in terms of relative densities in different strata. Three species of the *aurifasciatus*

Group (*P. acutirostris*, *P. leitensis*, and *P. longicrus*) are primarily terrestrial. Fifty percent or more of the specimens for each of these three species are from the forest-floor stratum. The percentages found in any one of the following microhabitats range from 2–18%: arboreal ferns, leaf axils of *Pandanus*, and leaves of trees or shrubs. The arboreal sites for these species were from 2–13 m above the forest floor. *Philautus schmackeri* exhibits a microhabitat distribution with the highest percentage on low shrubs.

The three species of the *surdus* Group (*emembranatus*, *surdus*, and *surrufus*) are much more arboreal, primarily in ferns and *Pandanus* (Table 3), 80–93% in shrub and arboreal microhabitats. The arboreal fern and leaf-axil sites for these three species ranged from 0.5–16+ meters above the forest floor. The limitation of *Philautus poecilus* to arboreal ferns or in leaf axils of *Pandanus* may be a result of insufficient sampling.

Egg-deposition sites for three Philippine species of *Philautus* (*surdus*, *schmackeri*, and one undetermined species) are arboreal ferns and leaf axils of *Pandanus*. Eggs are unpigmented. These species undergo direct development. *Philautus hosei* (*hosei* Group) most probably undergoes direct development, but the egg-deposition site is not known (Inger 1966, 1985b). Eggs of this species are uniformly dark gray. *Philautus kerangae* (*vermiculatus* Group) deposits eggs (one hemisphere pigmented) in water in *Nepenthes* pitchers where they undergo direct development (Dring 1987). Probably this mode characterizes all species of the genus.

Neither Inger (1989) nor Dring (1987) provided quantitative data relative to microhabitats occupied; but Inger noted that examples of *P. hosei*, *P. aurantium*, and *P. disgregus* were collected on shrubs and trees one-third to four meters above the ground. Inger (1966) noted that of six specimens of *P. aurifasciatus*, five were on low vegetation and one on the forest floor. Males of *P. ingeri*, *acutus*, *mjobergi*, *petersi*, *kerangae*, *umbra*, and *longicrus* were observed calling from the lower vegetation-stratum of the forest, one half to about three meters above the forest floor (Dring 1987). *Polypedates*.—Data on Philippine populations of *P. leucomystax* and *P. macrotis* indicate that both are residents of lowland forests, sea level to about 700–800 m. Both species have adapted to man-modified environs. *Polypedates leucomystax* is found in coconut groves, abaca groves, rice fields, grasslands, and wooded grasslands (Brown and Alcalá 1961). *Polypedates macrotis*, although more restricted to forests or the margins of clearings (Inger 1966), is also found in coconut groves near forests. *Polypedates leucomystax* occurs on many of the smaller islands that have little or no forest cover.

Eggs of both of these species are deposited in foamy masses attached to leaves of shrubs or trees overhanging permanent or temporary forest pools, or to grasses or rocks on banks bordering pools in open areas. Larvae fall or wriggle into the pools where development is completed (Alcalá and Brown 1956). *Polypedates otolithus* also deposits foamy egg masses on herbaceous plants near pools (Inger 1966).

*Rhacophorus*.—Data on three Philippine species (*R. appendiculatus*, *R. bimaculatus*, and *R. everetti*) indicate that they occur throughout the lowland (dipterocarp) forest from its lower limit near sea level to the upper edge at about 1000–1100 m. *Rhacophorus bimaculatus* is reported from the lower edge of the submontane forest in a few instances. *Rhacophorus pardalis* ranges deeply into the forest of the submontane zone (Brown and Alcalá 1961).

All specimens of *R. appendiculatus*, for which information is available, are from the foliage of trees. *Rhacophorus bimaculatus* and *R. pardalis* occur in the shrub stratum but rarely on the forest floor. Data for *R. everetti* are more limited but suggest that it is more frequent in the forest-floor stratum (Table 3). Very rarely are individuals of *Rhacophorus* species found in arboreal ferns or leaf axils of *Pandanus*.

*Rhacophorus pardalis* deposits its eggs in foam nests from which larvae fall into underlying pools where they complete development (Alcalá 1962, Brown and Alcalá 1983). Data on egg-deposition are not available for *R. appendiculatus* and *everetti*, but it is assumed that they also deposit their eggs in foam nests attached to substrates overhanging or adjacent to water pools or above slowly moving forest streams since larvae were found in such pools. Emerson (1991) erroneously stated that all rhacophorids share a common reproductive mode involving foam nests. This is true only for the genera *Polypedates* and *Rhacophorus* in the Philippines.

Larvae from an isolated forest pool in northern Borneo and from a pool in a mountain stream on Negros Island in the Philippines were tentatively identified with *Rhacophorus appendiculatus* (Inger 1985b, Alcalá and Brown 1982). Larvae of *R. pardalis* are reported from similar quiet pools (Alcalá 1962, Inger 1985b). No data on egg deposition or larval stages are available for *R. bimaculatus*, but a transforming juvenile with the tail not completely absorbed and clinging to a branch hanging over a forest stream is identified with this species. Bornean larvae, having a specialized oral disk and found in a forested mountain stream, are identified with *R. gauni*, a presumed close relative of *R. bimaculatus*.

#### PHYLOGENY AND ZOOGEOGRAPHY OF ASIATIC RHACOPHORIDS

Any hypothesis attempting to explain the present composition and distribution of the Philippine assemblage of rhacophorids must take into account: the original source of the Asiatic rhacophorids and dispersal from the source area, the evolutionary history of the Asiatic Rhacophoridae, dispersal routes between Borneo and the Philippines and distribution patterns in the Philippines, the geological history of the region, and the ecology of the Philippine species (see Heaney 1986, 1991; Heaney and Rickart 1990).

#### SOURCE AND EARLY DISPERSAL OF ASIATIC RHACOPHORIDAE

Duellman and Trueb (1985) hypothesized that rhacophorine and mantelline stocks were present in Gondwanaland before the rifts that separated the Madagascar-Seychelle-Indian components in the early Cretaceous (140–150 million years BP). The stocks giving rise to the current

TABLE 4. Summary of distribution patterns and endemism for the four rhacophorid genera that occur in the Philippines. (I = indigenous, E = endemic.)

Area	<i>Nyctixalus</i> 3 species		<i>Philautus</i> 64 species		<i>Polypedates</i> 13 species		<i>Rhacophorus</i> 57 species	
	I	E	I	E	I	E	I	E
India			27	22	2		11	6
Sri Lanka			6	2	3	2	3	2
China & Tibet			10	6	6	2	18	12
Japan							4	4
Mainland Southeast Asia <sup>a</sup>	1		8	5	5		16	8
Sumatra	1		2	2	4		7	2
Java	1	1	2	2	1		4	2
Borneo	1		12	11	4	2	13	6
Sulawesi					1		3	3
Philippines	2	1	9	8	3	1 <sup>b</sup>	4	

<sup>a</sup> Mainland Southeast Asia includes: Burma, Thailand, Laos, Vietnam, Cambodia, and the Malay Peninsula.

<sup>b</sup> *Polypedates hecticus* is probably not a valid species.

mantellid genera and *Boophis* in the Rhacophorinae were isolated (or persisted) in Madagascar. The rhacophorine stock remaining in Africa is represented by the genus *Chiromantis*. The rhacophorid stocks, ancestral to the seven genera occurring in Asia, were present in India when the Indian plate collided with the Eurasian plate in the Oligocene, about 35 million years BP. They propose over-water dispersal into the Philippines.

Channing (1989), like Duellman and Trueb (1985), attributed the present distribution of genera to vicariance, but dates it from the breakup of Pangaea about 200 million years ago. Channing believes that the Asiatic rhacophorids are polyphyletic in origin, and that the stocks ancestral to the present genera were in Pangaea.

Phylogenetic relationships of the genera of the Rhacophoridae were reported by Liem (1970) and Channing (1989). Liem's analysis placed the Asiatic *Buergeria* as the sister group to the other of the Asiatic genera plus the African *Chiromantis*, and *Philautus* as the sister groups to the remaining Asiatic genera. He placed *Nyctixalus* as the sister group to *Chiromantis* and *Polypedates* as the sister group to *Rhacophorus*. Channing, in his analysis of Liem's data, placed *Philautus* as the sister group of the African *Chiromantis*, *Rhacophorus* as the sister group of *Chirixalus*, and *Nyctixalus* as the sister group of *Theloderma*.

It is proposed that the rhacophorid genera expanded their ranges by dispersing eastward and later some of them southeastward through mainland Asia during the Oligocene. At least five of

the seven generic stocks reached the Sunda Shelf area, possibly as early as the late Oligocene. At least four genera subsequently dispersed to Borneo and the Philippines.

The nature and number of species associated with the generic stocks at the time of the early dispersal events are unknown. During the course of dispersal numerous speciation events occurred, resulting in current species richness and endemism for the subareas recognized in this study. The genus *Chirixalus* (seven species) is known from India, China, southeast Asia, Taiwan, and Japan. The genus *Theloderma* (eight species) is recorded from China, southeast Asia, and Sumatra. *Buergeria* (seven species) is recorded from Taiwan and the Ryukyu Islands. Generic ranges and subarea species richness and endemism patterns for the four genera that reach the Philippines are summarized in Table 4.

#### PHILIPPINE GEOLOGICAL HISTORY

The Philippines are a group of islands separated by the China Sea from the Asiatic mainland and separated by relatively narrow marine channels from Borneo to the southwest and the Sangihe chain and Sulawesi (Celebes) to the south. The latter, like the Philippine Islands, are part of Wallacea.

The Philippine Islands in their present form rose from the ocean floor since the Eocene. The older rock formations are capped by thick marine sediments (see Hamilton 1979, Heaney 1991). The oldest sub-aerial islands of the present Philippines are believed to be parts of Mindanao and

Luzon (late Oligocene to beginning Miocene, 25–30 million years BP). Palawan (as a group of small islands) probably became sub-aerial by the beginning of the Pliocene (6 million years BP); Leyte and Mindoro by the late Miocene to early Pliocene (8–10 million years BP); and Negros, Panay, and the Sulus by the middle to late Pliocene (2–4 million years BP). Pleistocene activities (uplift, volcanic, and tectonic) greatly altered the configuration of the islands.

Current hypotheses concerning Pleistocene sea-level changes propose a lower level of 160 m or possibly 200 m about 160,000 years BP and a lower level of 120 m about 16,000–18,000 years BP (Ollier 1985, Heaney 1985). These changes resulted in greatly enlarged aggregate islands and narrowing of persisting channels (Fig. 6). Mindoro and some of the smaller volcanic islands such as Camiguin, Tablas, Romblon, Sibuyan, as well as Siquijor, Camotes, Lubang, and Marinduque were not joined with any of the large island-aggregates in the late Pleistocene. Fragmentation of the larger islands, including Palawan and Mindanao on the entryways, also occurred during Pleistocene periods of reduced glaciation but are not yet adequately documented (see McLean 1980).

#### PHILIPPINE RHACOPHORIDS AND THEIR DISTRIBUTION PATTERNS

The living Philippine rhacophorids are a classic example of a depauperate island fauna. The fauna, as presently known, is an assemblage of 18 species compared to 30 in Borneo (the immediate source area) and 88 in the Asiatic mainland (the general source area). The present assemblage includes populations of species conspecific with populations in Borneo or elsewhere and endemic species. The endemics may be the result of speciation events that have taken place within the Philippines, or may be the only known populations of species that evolved elsewhere.

At least five generic stocks dispersed into the Sunda Island subarea. One (*Theloderma*) is presently known only from Sumatra in this subarea. The other four (*Nyctixalus*, *Philautus*, *Polypedates*, and *Rhacophorus*) are recorded throughout the Sunda Shelf Islands and have dispersed into the Philippines.

*Nyctixalus*.—This genus fits the category of a typical relict, based on its present peripheral range relative to probable area of origin, the limited

ranges (peripheral island areas for two of the species), and the small number of living species, three recognized (Inger 1985). It is represented in the Philippines by two, dipterocarp forest species, one on Palawan that also has populations on Borneo, Sumatra, and Malaya, and an endemic species in the greater Mindanao island group (Table 5). The Palawan species, *N. pictus*, is probably a relatively recent entry, perhaps as recently as the low sea-level period in the late Pleistocene. The ancestral stock to *N. spinosus* probably invaded the greater Mindanao group at an earlier point in time. Neither species has successfully colonized more peripheral Philippine islands.

*Polypedates* and *Rhacophorus*.—These two genera are represented in the Philippines by three and four species respectively. They have no endemic representatives. Both genera are highly successful in the sense that their current ranges extend from India (the ultimate source area) into the Philippines as compared to *Nyctixalus*, whose range is presently in peripheral subareas.

One species of *Polypedates* (*leucomystax*) is well adapted to cultivated fields and other man-controlled habitats. Dispersal opportunities resulting from these adaptations may account for its wide range from India to the Philippines and throughout the latter except for the greater Palawan group. Three additional species are present in Borneo, but only one of these (*P. macrotis*) is in the Philippines, and it is limited to greater Palawan and the Sulus (Tables 4 and 5). This shallow dispersal into the Philippines suggests a recent arrival, perhaps the time of most recent lower sea levels. This is supported by the fact that *P. macrotis* occurs along forest margins and some cultivated fields, a habitat that may enhance dispersal opportunities. *Polypedates hecticus* is a doubtful species.

There are no endemic Philippine species of *Rhacophorus*, but four of the 13 Bornean species are now known to occur in the Philippines. All are primarily in the dipterocarp forest habitat, although *R. pardalis* is also recorded from the submontane forest zone. *Rhacophorus everetti* is limited to the greater Palawan group of islands at the western entryway, but the other three species have dispersed from Mindanao into greater Negros and greater Luzon islands but not Mindoro (see Fig. 6 and Table 4). This expanded dispersal within the Philippines as compared to *Polypedates macrotis* suggests an earlier arrival

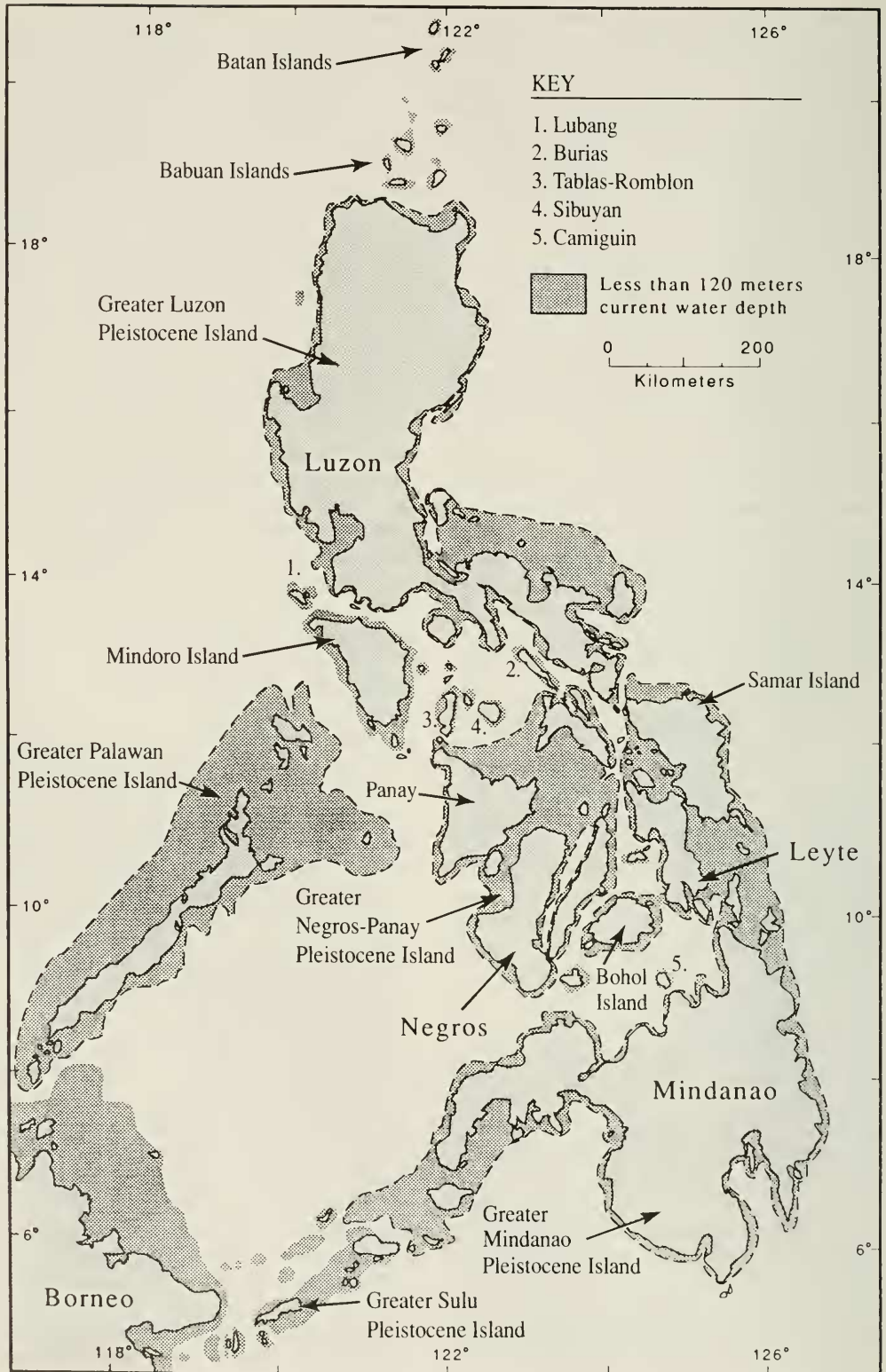


TABLE 5. Summary of distribution patterns and endemism for the four rhacophorid genera on Pleistocene and present-day islands of the Philippines. See text and Figure 7 for definition of Pleistocene islands. (I = indigenous, E = endemic.)

Area	<i>Nyctixalus</i> species		<i>Philautus</i> species		<i>Polypedates</i> species		<i>Rhacophorus</i> species	
	I	E	I	E	I	E	I	E
Philippine Archipelago	2	1	9	8 <sup>a</sup>	3 <sup>b</sup>	1 <sup>b</sup>	4	
Greater Palawan <sup>b</sup>	1		1		1		1	
Palawan	1		1		1		1	
Calait					1			
Busuanga					1			
Sulus <sup>c</sup>			1 <sup>a</sup>	1 <sup>a</sup>	2			
Greater Mindanao <sup>b</sup>	1	1	6	5	1		3	
Basilan	1		1		1			
Mindanao	1		5	4	1		3	
Dinagat							2	
Bohol	1		2		1		2	
Leyte <sup>c</sup>			1	1 <sup>d</sup>	1		1	
Samar <sup>c</sup>					2 <sup>a</sup>	1 <sup>a</sup>		
Camiguin <sup>b</sup>					1			
Greater Negros-Panay <sup>b</sup>					1		2	
Cebu					1			
Negros					1		2	
Panay <sup>c</sup>					1			
Masbate					1			
Siquijor							1	
Greater Luzon <sup>b</sup>			1		1		3	
Luzon			1		1		3	
Polillo <sup>c</sup>			1				1	
Mindoro			1	1	1			

<sup>a</sup> Doubtful species (*Philautus alticola* and *Polypedates hecticus*).

<sup>b</sup> Larger Pleistocene islands.

<sup>c</sup> Knowledge of the faunas of these islands is very limited.

<sup>d</sup> Range on both Bohol and Leyte.

in the Philippines. This is further supported by the fact that these *Rhacophorus* species are primarily forest species and thus have more restricted dispersal opportunities than does *P. macrotis*.

*Philautus*.—Like *Rhacophorus*, *Philautus* is highly successful in terms of both its extensive range and a large number of living species (Table 4). It differs in that speciation events in the subareas rather than dispersal events account primarily for species richness in each region. This genus has nine species in the Philippines, a greater diversity than occurs in any other rhacophorid genus. Eight of these are endemic there. Similarly, Borneo has 12 species with 11 endemic of

them. The one non-endemic species in each instance, *P. longicrus*, is the only species recorded from greater Palawan, the western entryway. The other eight species, all endemic, are in islands along the eastern entryway. Six species are limited to the greater Mindanao group, one has dispersed into the greater Luzon group, and one is endemic to Mindoro. The Philippine species are assigned to three of the five generic subgroups recognized by Dring (1987). The species of *Philautus* from Borneo and the Philippines also occur primarily in the submontane and montane forest habitats.

All of these factors support the hypothesis that the Philippine *Philautus* (except for *P. longicrus*)

←

FIGURE 6. Map of the Philippines (modified from Heaney 1990), showing present islands (pale stippled areas) and enlarged, late Pleistocene islands (dark stippled areas) based on the presumed extent of lower sea levels at that time.

are probably derived from at least two stocks that dispersed into greater Mindanao from Borneo somewhat earlier than did *Polypedates* or *Rhacophorus*. The limited dispersal within the Philippines of species of *Philautus* as compared to *Rhacophorus* is probably the result of reduced opportunities due to the more montane habitats occupied by the species of *Philautus*.

The paucity of rhacophorids on greater Palawan (four nonendemic species) compared to the rest of the Philippine islands is not readily accounted for based upon our present knowledge. Another peculiar feature of the rhacophorid fauna of greater Palawan is the absence of the widespread, highly adaptable *Polypedates leucomystax* that is widely dispersed through the rest of the Philippines.

Information on rhacophorid populations in the forests of Leyte, Samar, and some of the mountain areas of Luzon is needed to better understand some distribution patterns and to determine whether or not additional areas of endemism exist. This has some urgency, because the rain forests, especially the dipterocarp forests, are being cut at an accelerated rate on most of the large islands. The microhabitat preferences of the Philippine rhacophorids as well as their modes of reproduction, with the exception of *P. leucomystax* and *P. macrotis*, suggest that they will be endangered to the extent that the rain forests are depleted.

#### SUMMARY

Four of the seven recognized genera and 18 of the 159 recognized species of Asiatic rhacophorids occur in the Philippines. Ten of the species (including the doubtful *Philalutus aticola* and *Polypedates hecticus*) are endemic, and eight have ranges that include Borneo (the immediate source area), and in some instances, the Sunda Islands and even areas of mainland Asia.

*Nyctixalus* has the characteristics of a relict genus. *Philautus* is a highly successful genus in both number of species and its extensive range, from India through southern Asia to the Philippines. The genus is highly endemic in all subareas. For the Philippines, eight of nine species are endemic. *Polypedates* and *Rhacophorus* have even larger ranges than *Philautus* extending into southern temperate regions in eastern Asia. Excluding the very doubtful *Polypedates hecticus*, only two nonendemic species of *Polypedates* and

four nonendemic species of *Rhacophorus* occur in the Philippines.

These differences in species richness, endemism, and distribution patterns among the genera of Philippine rhacophorids are attributed to: probable differences in time of dispersal into the archipelago, differences in their ecology and its possible effects on dispersal within the Philippines, and geological events that also served to regulate dispersal opportunities.

#### RESUME

Quatre des septes genres reconnus et 18 des 159 espèces de rhacophorides asiatiques reconnues surviennent dans les Philippines. Dix des espèces (y compris le douteux *Philalutus aticola* et *Polypedates hecticus*) sont endémiques, et huit ont des rangées qui comprennent Borneo (l'immédiate source), et quelques fois, les Iles Sunda et même certains régions du continent asiatique.

*Nyctixalus* a les caractéristiques d'un genre veuf. *Philautus* est un genre plain de succès dans les deux espèces et sa vaste rangé, qui s'étend de l'Inde aux Philippines passant par le Sud de l'Asie. Le genre est fortement endémique dans toutes les sous-régions. Aux Philippines, huit sur neuf des espèces sont endémiques. *Polypedates* et *Rhacophorus* ont même des rangées plus étendues que *Philautus*, s'étendant en régions plus tempérées à l'Est de l'Asie. Sans compter le douteux *Polypedates hecticus*, seulement deux espèces non-endémiques de *Rhacophorus* surviennent dans les Philippines.

Ces différences dans la richesse des espèces, endémisme, et la distribution des modèles parmi les genres des rhacophorides Philippines sont attribuées a: de probables différences en temps dans la dispersion dans l'archipel, des différences dans leur écologie et ses effets possible dans la dispersion dans les Philippines et, des événements géologiques qui ont aussi servi à ajuster des opportunités dispersées.

#### ACKNOWLEDGEMENTS

We are deeply indebted to the American Philosophical Society for funds that enabled the senior author to complete a field trip to the Philippines in February 1992. We are indebted to E. N. Arnold (BMNH), A. Dubois (NMHN), K. Klemmer (SMF), R. Günther (ZMB), R. R. Inger (FMNH), E. Williams (MCZ), G. Zug and R. Crombie (USNM), C. J. McCoy (CM), and A. E.



Leviton (CAS) for permission to examine collections in their institutions. We also wish to thank our colleagues, A. Leviton, R. Drewes, and J. Vindum, for many helpful suggestions and for verification of some anatomical observations. We especially thank R. F. Inger and G. Zug for their thorough reviews and constructive comments during preparation of the final manuscript. We thank R. Heaney for permission to use the map that was modified for this paper and D. S. S. Liem for permission to reproduce Figure 1. Drawings and maps were prepared by P. Kaczmarek and C. Sudekum, California Academy of Sciences, and Panfilo Legaspi, Silliman University, Philippines.

## APPENDIX A

DISTRIBUTION OF RHACOPHORID FROGS  
IN THE PHILIPPINE ISLANDS

**Western Region.**—Palawan Island: *Nyctixalus picta*, *Philautus longicrus*, *Polypedates macrotis*, *Rhacophorus everetti*. Balabac Island: *Philautus longicrus*, *Polypedates macrotis*. Dumarán Island: *Polypedates macrotis*. Busuanga Island. *Polypedates macrotis*. Calauit Island: *Polypedates macrotis*.

**Southern and Eastern Region.**—Bongao Island (Sulus): \* *Philautus alticola*. Jolo Island (Sulus): *Polypedates macrotis*, *P. leucomystax*. Mindanao Island: *Nyctixalus spinosus*, *Philautus acutirostris*, *P. emembranatus*, *P. poecilus*, *P. surdus*, *P. surrufus*, *Polypedates leucomystax*, *Rhacophorus appendiculatus*, *R. bimaculatus*, *R. pardalis*. Basilan Island: *Nyctixalus spinosus*, *Philautus acutirostris*, *Rhacophorus appendiculatus*, *R. bimaculatus*. Camiguin Island: *Polypedates leucomystax*, *Rhacophorus pardalis*. Dinagat Island: *Rhacophorus appendiculatus*, *R. pardalis*. Bohol Island: *Nyctixalus spinosus*, *Philautus leytensis*, *P. surdus*, *Polypedates leucomystax*, *Rhacophorus appendiculatus*, *R. bimaculatus*, *R. pardalis*. Leyte Island: *Philautus leytensis*, *Polypedates leucomystax*. Samar Island: \* *Polypedates hecticus*, *P. leucomystax*. Poro Island: *Polypedates leucomystax*. Pacijan Island: *Polypedates leucomystax*.

**Central Region.**—Cebu Island: *Polypedates leucomystax*. Masbate Island: *Polypedates leucomystax*. Cagayan Island: *Polypedates leucomystax*. Siquijor Island: *Polypedates leucomystax*, *Rhacophorus pardalis*. Calagaán Island: *Polypedates leucomystax*. Carabao Island: *Polypedates leucomystax*. Gigante South Island: *Polypedates leucomystax*. Guimaras Island: *Polypedates leucomystax*. Inanipulagan Island: *Polypedates leucomystax*. Pamionlon Island: *Polypedates leucomystax*. Pan de Azúcar: *Polypedates leucomystax*. Sicogon Island: *Polypedates leucomystax*. Negros Island: *Polypedates leucomystax*, *Rhacophorus appendiculatus*, *R. pardalis*. Panay Island: *Polypedates leucomystax*.

**Northern Region.**—Luzon Island: *Philautus surdus*, *Polypedates leucomystax*, *Rhacophorus bimaculatus*, *R. pardalis*. Polillo Island: *Philautus surdus*, *Rhacophorus pardalis*. Mindoro Island: *Philautus schmackeri*. Tablas Island: *Polypedates leucomystax*. Caluya Island: *Polypedates leucomystax*. Semirara Island: *Polypedates leucomystax*. Sibay Island: *Polypedates leucomystax*.

\* doubtful species

## APPENDIX B

## SPECIMENS EXAMINED

For brevity, only island names and museum numbers are provided. Precise locality data are available from the museum catalogs.

*Nyctixalus spinosus*.—Basilan I.: CAS 60168, 60379; Mindanao I., Agusan del Norte Province, west slopes of Mt. Hilong-hilong: CAS 139319, 133561, 133629-32, Bunawan: CM 3420 (holotype of *Hazelia spinosa*); Bohol I., about 10 km SE of Sierra Bullones: CAS-SU 22788.

*Philautus acutirostris*.—Mindanao I., eastern region: ZMB 5690 (holotype of *Ixalus acutirostris*); Mt. Hilong-hilong, Agusan del Norte Prov.: CAS 133140, 133164-7, 133211-2, 133259, 133262, 133289-90, 133298-300, 133305-6, 133308-9, 133311-2, 133334-6, 133394, 133649-50; west side of Dapitan Peak, Zamboanga del Norte Prov.: CAS-SU 20883-4, 20886-7, 20890-7, 20900, 20903, 20912-3; west side of Dapitan Peak, Misamis Occ. Prov.: CAS-SU 20644, 20646-58, 20660, 20686-90, 20692-4, 20695-706, 20728-30, 20780-92, 20798-801, 20803-6, 20851, 20861-7. Saub, Cotobato Coast: MCZ 23194-97; Davao Prov., Mt. Apo: USNM 34781 (holotype of *Philautus woodi*), USNM 34782 (paratype); Abungabung, Basilan I.: CAS 60145 (holotype of *Philautus basilanensis*); MCZ 14467-68 (paratypes of *Philautus basilanensis*).

*Philautus leytensis*.—Bohol I., Sierra Bullones (Dusita) area: CAS-SU 22775, 22819-53; Can-

taub area CAS 139011-15; Leyte I., Calabian: MCZ 23192; BMNH 96.12.11.32 (holotype).

*Philautus longicrus*.—Palawan I.: BMNH 1947.2.6.29 (cotype); CAS 64093; Malabo (near Central Pk.): CAS-SU 24174; 2 km W of Iwahig: CAS-SU 24246; 3–5 km SW of Iwahig: CAS-SU 24211-12, 24218, 24236, 24272; south slope of Thumb Peak: CAS-SU 24204-210, 24220-25, 24227-35, 24237-39, 24241, 24243-44, 24247-60, 24262-71, 24273-79, 24286, FMNH 105501-02; Brooke's Point: FMNH 51351.

*Philautus schmackeri*.—Mindoro I., Mindoro Occidental Prov., Mangarin: CAS-SU 9840; Mindoro Oriental Prov., west of Tarogin Barrio about 30 km south of Calapan: CAS-SU 22314, 22345-48, 22363-64, 22379, 22394, 22507, 22611, 22623-24, 22645-51; southeast slope of Barawan Peak: CAS-SU 16859-86, 22315-24, 22349-56, 22365-78, 22381-93, 22395-415, 22459-63, 22470-80, 22495-506, 22508-75, 22606-10, 22613-19, 22625-28, 22644, 22652-76, 22735-39, 22750-73, 24054; Mt. Halcon: SMF 7035 (holotype); south slope of Mt. Halcon: CAS-SU 22467-69, 22490-94; east slope of Mt. Halcon: CAS-SU 22605, 22629-41, 22642-43; Mt. Dulangan: BMNH (syntypes of *Ixalus mindorensis*).

*Philautus emembranatus*.—Mindanao I., Davao Prov., Mt. McKinley: FMNH 50684 (holotype); Agusan del Norte Prov., south and southwest slopes of Mt. Hilonghilong: CAS 133237, 133252, 133305-06, 183415; Misamis Occidental Prov., W slope of Dapitan Peak: CAS-SU 20338, 20341, 20349, 20356, 20362-63, 20366, 20368, 20371-73, 20949, 20961, 21175, 21641-42; Zamboanga Prov., slopes of Dapitan Peak: CAS-SU 20365, 21192, MCZ 39054; Bukidnon Prov., Mt. Kitanglad: FMNH 250626-28.

*Philautus surdus*.—Luzon I.: ZMB 4920 (holotype of *Polypedates surdus*); Mt. Maquiling: MCZ 23280-83, 23285-87; 87400-17; Polillo I.: MCZ 14473 and CAS 62254 (paratypes of *Philautus williamsi*); Mindanao I., Davao Prov., Mt. McKinley: FMNH 50683 (holotype of *lisso-brachius*); Agusan del Norte Prov., Mt. Hilonghilong: CAS 133263, 133343, 133523, 133534, 133646-47, 133791, 133793, 182565, 182568; Zamboanga del Norte Prov., 6–9 km southeast of Buena Suerte on Dapitan Peak: CAS-SU 20353-55, 20643; MCZ 39055; Misamis Occidental Prov., 8–22 km southeast of Buena Suerte on Dapitan Peak: CAS-SU 20337, 20339, 20342-

46, 20348-50, 20356, 20359-60, 20370, 20940-41, 20945, 21061, 21069, 21144, 21176-80, 21185, 21651-53, 21655, 21665-66, 21669, 21677-80; Bohol I., Sierra Bullones area, Teachers Park: CAS-SU 23351-52; Dusita (10–13 km SE of Sierra Bullones): CAS-SU 23336, 23349-50, 23437, CAS 145700-701; Cantaub (9–16 km SE of Sierra Bullones): CAS-SU 17143-45, 22811-12, 22814, 23341-49, 23353-54, CAS 136845, 136870, 136875, 136887, 139016-139018.

*Polypedates leucomystax leucomystax*.—Philippines, Alabat I.: CAS-SU 3795; Bohol I.: CAS 139029; Cagayan I.: CAS 157189-208; Caluya I.: CAS 127512-14, 127540-58, 127592-95, 127608-10, 127647-49, 127657, 127670-76, 127680-97; Calagaan I.: CAS 124158, 124192, 124204; Camiguin (south) I.: CAS-SU 23045-63, 24055, 24111-13; Carabao I.: CAS 128114; Cebu I.: CAS-SU 16501, 23863-64, 24287, CAS 129130, 131915-18, 131969, 136833-36; Gigante South I.: CAS 125034-37; Guimaras I.: CAS 125342-43; Inampulugan I.: CAS-SU 23950-51, 23959-60, 23964-65; Jolo I.: CAS 60632-51; Leyte I.: CAS-SU 9388, 14817; Luzon I.: CAS-SU 9825-30, 14057-60, 14075, 14760-63, 14791-97, CAS 15575-76, 15667-78, 15699-706, 15713, 15730, 42012-20, 61044-47, 61368-74, 61388-460, 61655-70, 73876-78, 140070; Masbate I.: CAS 144275-79, 144281, 144320; Mindanao I.: CAS-SU 13970-75, 13991, 14770-79, 14799-800, 16239-42, 16493, CAS 15722-24, 133626-28, 133643, 133667-71, 133712-25, 137520-24; Mindoro I.: CAS-SU 11117-19, 13976-90, 14063-74, 14076, 16237-38, 16246, 22113-24, 22244-45, 22261-64, 22313, 22589, CAS 73879; Negros I.: CAS-SU 9833-39, 10795-97, 14765-69, 14780-90, 16210-35, 17719-20, 18108, 18141-43, 23529-37, CAS 92960-62, 92981, 131835, 139274, 154185; Pacijan I.: CAS 124025-26, 124339-42, 124352-56; Pan de Azucar I.: CAS 124176, 125031-32; Panay I.: CAS-SU 11113-16, 14764, CAS 137599; Poro I.: CAS 124521; Semirara I.: CAS 127841; Sibay I.: CAS 127721-26; Sicogon I.: CAS 124110-13, 124420, 124422-25, 124581; Tablas I.: CAS 137274-80, 137297, 139209.

*Polypedates macrotis*.—Philippines, Jolo I.: CAS 60684 (holotype of *Polypedates linki*), 60804; Bud Dako Mountain: CAS 60630-31; Palawan I.: CAS 64074, 64089-92; Iwahig area: MCZ 14436-38; 8 km S of Iwahig: CAS-SU 21640; Malabosog Creek, 95 km N of Puerta

Princesa: CAS 157330-42; Brooke's Point: MCZ 14439-50; Calauti I.: CAS 180833; Dumaran I.: MCZ 14435; Busuanga I.: CAS-SU 13969.

*Rhacophorus appendiculatus*.—Philippine Is.: BMNH 1947.2.9.17 (cotype); Negros I., Bagtic River Valley: CAS-SU 18114-23; Bohol I., Sierra Bullones area: CAS 10216, CAS-SU 22818; Leyte I.: CAS-SU 14750-54; Basilan I.: CAS 60169-74; Polillo I.: CAS 62261; Mindanao, Cotabato: CAS 64078-86; Philippines: CAS-SU 14755-59.

#### LITERATURE CITED

- AHL, E. 1927. Zur systematic der asiatischen arten der froschgattung *Rhacophorus*. Sitzber. Gesell. Naturf. Berlin 1927: 35-47.
- . 1931. Anura III, Polypedatidae. Das Tierreich 55: 1-478.
- ALCALA, A. C. 1962. Breeding behavior and early development of frogs of Negros, Philippine Islands. Copeia 1962: 679-726.
- ALCALA, A. AND W. C. BROWN. 1956. Early life history of two Philippine frogs with notes on deposition of eggs. Herpetologica 12:241-246.
- . AND ———. 1982. Reproductive biology of some species of *Philautus* (Rhacophoridae) and other Philippine anurans. Kalikasan, Philipp. J. Biol. 11:203-226.
- BARTLETT, E. 1894. Notes on the Batrachians or frogs and toads of Borneo and the adjacent islands. Pp. 7-14 (reprint) in The Ethnological, Zoological, and Botanical Note Book of Sarawak, 1896, E. Bartlett, ed., Domingo J. J. Rodrigues Co., Kuching, Sarawak.
- BERRY, P. Y. 1975. The Amphibian Fauna of Peninsular Malaysia. Tropical Press, Kuala Lumpur. 1-127.
- BOETTGER, O. 1886. Augzählung der von den Philippinen bekannten Reptilien und Batrachier. Ber. Senck. Naturf. Ges. 1886:91-134.
- . 1892. Katalog der Batrachier Sammlung im Museum der Senckenbergischer naturforschenden Gesellschaft in Frankfurt am Main. Gebruder Knauer, Frankfurt a. M., 1-73.
- . 1899. *Rhacophorus rizali* ein neuer Baumfrosch von Mindanao, nebst Fundortnotizen von den Philippinen überhaupt. Abh. Ber. Mus. Dresden, 1899, no. 1:1-3.
- BOULENGER, G. A. 1882a. Catalogue of the Batrachia Saliencia s. Ecaudata in the Collection of the British Museum. Taylor & Francis, London, ed. 2:1-503.
- . 1882b. Description of a new genus and species of frogs of the family Ranidae. Ann. Mag. Nat. Hist. (5) 10:35.
- . 1891. Descriptions of new reptiles and batrachians. Ann. Mag. Nat. Hist. (6) 7:279-283.
- . 1894. On the herpetological fauna of Palawan and Balabak. Ann. Mag. Nat. Hist. (6) 14:81-90.
- . 1897. Descriptions of New Malay Frogs. Ann. Mag. Nat. Hist. (6) 19:106-110.
- BROWN, W. C. AND A. C. ALCALA. 1961. Populations of amphibians and reptiles in the submontane and montane forests of Cernuos de Negros, Philippine Islands. Ecology 42:628-636.
- . AND ———. 1964. Relationship of the herpetofaunas of the non-dipterocarp communities to that of the dipterocarp forest on southern Negros Island, Philippines. Senckenberg. Biol. 45:591-611.
- . AND ———. 1982. Reproductive biology of some species of *Philautus* (Rhacophoridae) and other Philippine anurans. Philipp Kaliksan. J. Biol. 11:203-226.
- . AND ———. 1983. Modes of reproduction of Philippine Anurans. Pages 415-428 in Advances in Herpetology and Evolutionary Biology. A. G. J. Rhodin and K. Mujata, eds. Harvard Univ. Press, Cambridge.
- CHANNING, A. 1989. A re-evaluation of the phylogeny of Old World tree frogs. S. Afr. Tydskr. Dierk. 24 (2):116-131.
- DRING, J. 1987. Bornean tree frogs of the genus *Philautus* (Rhacophoridae). Amphibia-Reptilia 8:19-47.
- DUBOIS, A. 1981. Liste des genres et sousgenres nominaux de Ranoidea (Amphibiens Anoures) du monde, avec identification de leurs Espèces-Types: Conséquences nomenclaturales. Monit. Zool. Ital. N. S., Suppl. 15:225-284.
- . 1987. Miscellanea taxinomica batrachologica (I). Alytes 5:7-95.
- DUJELMAN, W. E. AND L. TRUEB. 1985. Biology of Amphibians. McGraw-Hill Book Co., New York. 1-670.
- DUMÉRIL, A. M. C. AND G. BIBRON. 1841. Erpetologie générale ou histoire naturelle complète des Reptiles. Librairie Roret, Paris 8:1-792.
- EMERSON, S. B. 1991. The ecomorphology of Bornean tree frogs (family Rhacophoridae). Zool. J. Linn. Soc. 101:337-357.
- FISCHER, J. G. 1885. Über eine Kollektion von Amphibien und Reptilien aus Sudost-Borneo. Archiv. Naturg. 1885:41-72.
- FITZINGER, L. 1843. Systema Reptilium. Fasc. Amblyglossae. Braumüller and Seidel, Wien. 1-106.
- GISTEL, J. 1848. Naturgeschichte des Thierreichs für höhere Schulen. Stuttgart, Hoffmann. 1-216.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183-190.
- GRAVENHORST, J. L. C. 1829. Deliciae Musei Zoologici Vratislaviensis. Fasciculus primus continens chelonios et Batrachia. Lipsiae 1829:1-106.
- GÜNTHER, A. 1859. Catalogue of the Batrachia Saliencia in the collection of the British Museum. Taylor and Francis, London. 1-160.
- HALLOWELL, E. 1860. Report upon the reptilia of the North Pacific exploring expedition under command of Capt. John Rodgers, U. S. N. Proc. Acad. Nat. Sci. Philadelphia 12: 480-510.
- HAMILTON, W. 1979. Tectonics of the Indonesian Region. U. S. Geol. Surv. Prof. Pap. 1078:1-345.
- HEANEY, L. R. 1985. Zoogeographic evidence for middle and late Pleistocene land bridges to the Philippine Islands. Mod. Quaternary Res. SE Asia 9:127-143.
- . 1986. Biogeography of mammals in southeast Asia: estimates of rates of colonization, extinction and speciation. Biol. J. Linn. Soc. 28:127-165.
- . 1991. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae). Bull. Amer. Mus. Nat. Hist. No. 206:145-167.
- HEANEY, L. R. AND E. A. RICKART. 1990. Correlations of clades and clines: Geographic, elevational, and phylogenetic distribution patterns among Philippine mammals. Pp. 321-332 in Vertebrates in the Tropics. G. Peters and R. Hutterer, eds. Mus. Alexander Koenig, Bonn.
- HOFFMAN, A. C. 1932. Researches relating to the validity

- of the South African Polypedatidae (Rhacophoridae) as an autonomous family of the anura. *S. Afr. J. Sci.* 29:562-583.
- ILLIGER, J. K. W.. 1798. Verzeichniss der Käfer Preussens. Johann Jacob Gebaux, Halle. 1-510.
- INGER, R. F. 1954a. Systematics and zoogeography of Philippine amphibia. *Fieldiana: Zool.* 33:181-531.
- . 1966. The systematics and zoogeography of the amphibia of Borneo. *Fieldiana: Zool.* 52:1-402.
- . 1985a. Rhacophoridae of Asia. Pages 525-549 in *Amphibian Species of the World*, D.R. Frost, ed. Allen Press, Lawrence, Kansas.
- . 1985b. Tadpoles of the forested regions of Borneo. *Fieldiana: Zool. (new series)* 26:1-89.
- . 1989. Four new species of frogs from Borneo. *Malayan Nat. J.* 42:229-243.
- INGER, R. F. AND R. B. STEUBING. 1992. The montane amphibian fauna of northwestern Borneo. *Malayan Nat. J.* 46:41-51.
- INGER, R. F. AND F. L. TAN. 1990. Recently discovered and newly assigned frog larvae (Ranida and Rhacophoridae) from Borneo. *Raffles Bull. Zool.* 38(1):3-9.
- KAMPEN, P. N. VAN. 1907. Amphibien des Indischen Archipels. Pp. 383-416 in *Zool. Ergebn. Reise Niederl. Ost-Indien*, M. Weber, Vol. 4.
- . 1923. The Amphibia of the Indo-Australian Archipelago. E. J. Brill, Leiden. 1-304.
- KUHL, H. AND J. C. VAN HASSELT. 1822. Uittreksels uit brieven van de Heeren Kuhl en van Hasselt aan de Heeren C. J. Temminck, T. van Swinderen en W. de Haan. *Algemeene Konst en Letter-Bode* 7:99-104.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802-832.
- LIEM, D. S. S. 1970. The morphology, systematics and evolution of the Old World tree frogs. (Rhacophoridae and Hyperoliidae) *Fieldiana Zool.* 57:1-145.
- MARX, K. W. 1975. A substitute name, *Edwardtayloria*, for a genus of tree frogs from southeast Asia. *Sci. Publ. Sci. Mus. Minnesota* 2:1-3.
- MCLEAN, R. F. 1980. Spatial and temporal variability of external physical controls on small ecosystems. Pages 149-175 in *Population-environment in tropical islands: the case of eastern Fiji*, UNESCO 1980, MAB Technical Notes 13.
- Ogilby, C. D. 1837. Remarks on some rare or undescribed ruminants in the Societies' collection. *Proc. Zool Soc. London* 1837:119-121.
- OLLIER, C. D. 1985. The geological background to prehistory in island Southeast Asia. *Mod. Quaternary Studies in Southeast Asia.* 9:25-42.
- PETERS, W. 1863. Mittheilungen über neue Batrachier. *Monatsber. Akad. Wiss. Berlin.* 1863:445-470.
- . 1867. Herpetologische Notizen. *Monatsber. Akad. Wiss. Berlin.* 1867:13-37.
- . 1871. über neue Reptilien aus Ostafrika und Sarawak (Borneo), vorzüglich aus der Sammlung deo Hrn. Marquis J. Doria zu Genua. *Monatsber. Akad. Wiss. Berlin* 1871:566-581.
- RABOR, D. S. AND A. C. ALCALA. 1959. Notes on a collection of amphibians from Mindanao Island, Philippines. *Philipp. J. Sci.* 88:335-344.
- RIDE, W. D. L. 1985. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature. 1-338.
- SCHEGEL, H. 1826. Notice sur l'herpetologie de l'île Java; par M. Boie. *Bull. Sci. nat. Geol.* 9:233-240.
- . 1837-1844. Abbildungen neuer oder unvollständig bekannter Amphibien. . . Conservator des Niederländischen Reichs-Museum. Verlag v. Arnz & Company 1837-1844:1-151 + 50 pls.
- STEJNEGER, L.. 1905. Three new frogs and one new gecko from the Philippine Islands. *Proc. U. S. Nat. Mus.* 28:343-348.
- . 1907. Herpetology of Japan and adjacent territory. *Bull. U. S. Nat. Mus.* 58:1-577.
- TAYLOR, E. H. 1920. Philippine Amphibia. *Philipp. J. Sci.* 16:213-359.
- . 1921. Amphibia and Turtles of the Philippine Islands. *Dept. Agri. and Nat. Res. Bur. Sci., Pub.* 15:1-193.
- . 1922a. Additions to the herpetofauna of the Philippine Islands I. *Philipp. J. Sci.* 21:161-206.
- . 1922b. Additions to the herpetofauna of the Philippine Islands. II. *Philipp. J. Sci.* 21:257-303.
- TSCHUDI, J. J. 1838. Classification der Batrachien, mit Berücksichtigung der fossilen thiere. *Mem. Soc. Sci. Nat. Neuchatel.* 2:1-99.
- VILLADOLO, D. V. AND N. DEL ROSARIO. 1930. Studies on the development and feeding habits of *Polypedates leucomystax* (Gravenhorst), with a consideration of the ecology of the more common frogs of Los Banos and vicinity. *Philipp. Agriculturist* 18:475-503.
- VOGT, T. 1911. Beitrag zur Amphibienfauna der Insel Formosa. *Sitzsber. Gesell. Naturf. Berlin.* 1911:179-184.
- WALCOTT, C. D. 1920. Cambrian Geology and Paleontology. IV. Middle Cambrian Spongiae. *Smithson. Misc. Coll.* 67:261-364.
- WOLF, S. 1936. Revision der Untergattung *Bull.* *Raffles Mus.* No. 12:137-217.
- WIEGMAN, A. F. A. 1835. Amphibien. *Nova Acta Acad. Leop. Carol.* 17:225-261.